The Whale Lice (Amphipoda: Cyamidae) of the Northeastern Pacific Region

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ABSTRACT

This study treats the systematics and host relationships of cyamid ectoparasites of whales (Cetacea) of the northeastern Pacific region. The caprellidean amphipod family Cyamidae is revised, and keys to all component genera, subgenera and regional species are provided. ***Orcinocyamus*** n. g., ***Cyamus (Apocyamus)*** n. subg., and ***Cyamus (Mesocyamus)*** n. subg., ***Cyamus (Mesocyamus) mesorubraedon*** n. sp., and ***Cyamus (Apocyamus) eschrichtii*** n. sp., are newly defined, and subgenus ***Cyamus (Paracyamus)*** G. O. Sars is revived. Redescribed and refigured, wholly or in part, are: *Cyamus (Cyamus) ceti* (L.) Lamarck, *C. (Cyamus) monodontis* Lütken, *C. (Cyamus) erraticus* R. de Vauzème, *C. (Cyamus) ovalis* R. de Vauzème, *C. (Cyamus) gracilis* R. de Vauzème, *Cyamus (Paracyamus) balaenopterae* K. H. Barnard, *C. (Paracyamus) boopis* Lütken, *C. (Mesocyamus) catodontis* Margolis, *C. (Mesocyamus) orubraedon* Waller, *C. (Apocyamus) scammoni* Dall, *C. (Apocyamus) kessleri* Brandt, *Neocyamus physteris* (Pouchet); *Isocyamus delphinii* (Guérin-Méneville), *I. globicipitis* Lütken, and *Platycyamus flaviscutatus* Waller. Analysis of a broad range of characters and char-acter states suggests that the phyletic position of the Cyamidae within the Caprellidea may be closer to Capro-gammaridae-Caprellidae than to the Caprellinoididae-Phtisicidae evolutionary grouping as suggested elsewhere. Phyletic classification of the Cyamidae accords reasonably well with that of the host Cetacea. Thus, species of the most primitive genus *Cyamus* (and subgenera) are found mainly on the most primitive whales (Mysticeti) whereas the more advanced genera of cyamids (*Isocyamus, Neocyamus, Orcinocyamus, Syncyamus*, and *Scutocyamus*) occur only on the more advanced Odontoceti. Some species of *Cyamus* occur on more primitive members of the Odontoceti (e.g., on *Physeter, Berardius*, Monodontidae) but host size and life style may also prove significant factors here. Two distinct groups of advanced cyamids recognized herein could support other evidence for polyphyletic origin within the Odontoceti. However, such conclusions would seem premature since many host-parasite relationships remain undiscovered.

Introduction

The caprellidean family Cyamidae comprises a major parasitic group of amphipod crustaceans. Some gammaridean family groups (e.g., Opisidae, Trischizostomatidae, Lafystiidae) are ectoparasites of fishes, *Hyachelia* (Talitroidea) occurs on marine turtles, and members of the suborder Hyperiidea attach to pelagic coelenterates and tunicates (Bousfield & Kabata 1988). Only the Cyamidae, consisting of seven genera and 34 known species, are ectoparasites of Cetacea. Three genera and eight species have previously been reported from the Northeastern Pacific, of which two genera and five species have been noted on whales in North American Pacific waters. The purpose of this study is to update knowledge of the systematics and host-parasite relationships of this regional crustacean group.

Early studies on Cyamidae in the northeastern Pacific marine region commenced with the work of Dall (1872a, b, 1874). From Californian waters he described as new species *Cyamus suffusus* (ex humpback whale, *Megaptera nodosa*) and *Cyamus scammoni* (ex California Gray whale, *Eschrichtius gibbosus*). From Alaskan waters Dall described the new species *Cyamus tentator* and *C. gracilis* [(ex Pacific right whale (=black right whale) *Balaena sieboldii* (= *B. glacialis*)], as well as *C. mysticeti* (ex bowhead whale, *Balaena mysticetus*). Illustrations of *C. suffusus*, *C. scammoni*, and *C. mysticeti* appear in Scammon's (1874) account of North American Pacific Cetacea. Lütken (1887), after reexamining Dall's specimens, considered *C. tentator* identical with *C. ovalis* R. de Vauzème, 1834, *C. mysticeti* Dall identical with *C. monodontis* Lütken, 1870 (= *C. ceti* Linnaeus, 1758) and *C. suffusus* identical with *C. pacificus* Lütken, 1873. This last species was described by Lütken (1873) from an unidentified cetacean caught off the Pacific coast of Central America. Lütken (1873, 1887) further considered *C. pacificus* as probably identical with *Cyamus boopis* Lütken, 1870, a view upheld by later workers. Sars (1895) created the new genus *Paracyamus* for *C. boopis*. Subsequently *Cyamus gracilis* was transferred to this genus by Barnard (1932). *Paracyamus boopis* has also been recorded from the humpback whale in British Columbia by Cornwall (1928) and in Alaskan waters by Scheffer (1939). However, the genus *Paracyamus* was recently placed in synonomy of *Cyamus* by Margolis (1959).

In the northwestern Pacific ocean, several species

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have been recorded from Kamchatka, Korea, and Japan. A. Brandt (1871) believed he had rediscovered *Sirenocyamus rhytinae* J. F. Brandt, 1846. Later he noted its great similarity to *Cyamus ovalis*, attached to a piece of skin of what he believed to be *Rhytina borealis* (the extinct sea cow), which was preserved in the St. Petersburg museum. The animal was apparently caught off Kamchatka. *Cyamus ovalis* was later recorded by A. Brandt (1872) from *Balaena japonica* (probably identical with *B. glacialis*) in Kamchatka waters and thereby considered *C. rhytinae* as only a variety of *C. ovalis*. Lütken (1873) came to the conclusion that *C. rhytinae* of A. Brandt, 1871, was identical with *C. ovalis* and the piece of skin from which Brandt recovered his specimens was actually from *B. japonica* and not *R. borealis*. The original amphipod parasite of *R. borealis* was described by Steller in 1751 and named *Sirenocyamus rhytinae* by J. F. Brandt in 1846. He considered this parasite to be closely related to the genus *Cyamus*. Lütken (1873) temporarily placed the species in the genus *Cyamus*, but its true systematic position remains in doubt. Cognizant of the descriptions of Steller (loc. cit.) and J. F. Brandt (loc. cit.), these amphipods doubtfully belong to the genus *Cyamus* or even the family Cyamidae. Lütken (1873) also listed *C. gracilis* (i.e., *Paracyamus gracilis*) as a parasite of *Balaena japonica* in the seas off Kamchatka.

Andrews (1914) reported *C. scammoni* as parasitic on the gray whale in Korean waters. From Japanese seas Ishii (1915) recorded a species of *Cyamus* from *Berardius bairdi*, which Iwasa (1934) believed was probably *P. boopis*. The latter author redescribed *C. ovalis* and *C. erraticus* R. de Vauzème, 1834, taken from *B. glacialis*. *Cyamus elongatus* was newly described from the humpback whale by Hiro (1938). The latter also recorded *C. globicipitis* Lütken, 1873 (= *Isocyamus delphini* (Guérin-Méneville, 1836) from *Globicephalus scammoni* in Japanese waters.

A more recent account of cyamid ectoparasites from the North American Pacific coast was given by Margolis & Dailey (1972), and the world cyamid fauna updated by Berzin & Vaslova (1982). Fourteen cyamid species are here recorded from whales caught off the British Columbia coast and landed at Coal Harbour, and from other localities along the coast of British Columbia (Table I, p. 110, and species accounts). Two species *Cyamus (Mesoyamus) mesorubraedon* and *Cyamus (Apocyamus) eschrichtii*, are described as new to science. The specimens were collected by Mr. G. C. Pike, unless otherwise noted. All specimens formerly in the collections of Dr. Leo Margolis, Pacific Biological Station, Nanaimo, B. C., are now in the Parasitology Collections of the Canadian Museum of Nature (CMN), Ottawa.

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Systematics

Family Cyamidae Rafinesque, 1817
Cyamidae Lütken 1873; Sars 1895; Chevreux & Fage 1925; Stephensen 1942; Margolis 1954; Leung 1967; Grüner 1975; Laubitz 1993; Krapp-Schickel 1993.

Type genus: *Cyamus* Latreille, 1796
Genera: *Orcinocyamus* new genus; *Isocyamus* Gervais & Van Beneden, 1859; *Neocyamus* Margolis, 1955; *Platycyamus* Lütken, 1870; *Syncyamus* Bowman, 1955; *Scutocyamus* Lincoln & Hurley, 1974.

Diagnosis: Body (peraeon) short, wide, dorsoventrally depressed, usually smooth dorsally, often with short ad-hesion spines ventrally. Peraeon 1 usually fused with head. Eyes small, dorsal. Antenna 1 short; antenna 2 very short or rudimentary. Buccal mass small, mouthparts reduced. Upper lip usually notched apically, lobes variously asymmetrical. Lower lip, inner lobes present, often fused. Mandible lacking palp; molar rudimentary. Maxilla 1, palp small, 1-segmented. Maxilla 2 small, plates very small or fused. Maxilli-ped basal segments often fused medially; palp often lacking.

Gnathopods 1 & 2 strongly subchelate, unequal in size, slightly sexually dimorphic; segments 3 & 5 often fused with 2 & 4 respectively. Peraeopods 3 & 4 lacking. Peraeopods 5-7 short, stout, powerfully clasping (raptorial) in form. Peraeon segments 3 & 4 each with paired coxal gills, simple or ramified, usually with accessory gills. Pleopods (one pair) rudimentary and fused in male, lacking in female. All species ectoparasitic on Cetacea.

Remarks: The diagnosis is adapted partly from Sars (1895) Chevreux & Fage (1925), Grüner (1975) and Krapp-Schickel (1993) whose key (loc. cit.), involving presence of a mandibular palp appears to have been a printing lapsus (pers. comm.).

Cyamus Latreille, 1796

Subgenera: *Cyamus* (L.) Lamarck, 1801 (nominate); *Paracyamus* G. O. Sars, 1895; ***Mesocyamus***, new subgenus (p. 82); ***Apocyamus***, new subgenus (p. 87).

Diagnosis: Mostly relatively large animals, ectoparasitic on large whales, mainly Mysticeti, Ziphiidae, Monodontidae, and Physeteridae.

Body variable, often slender in males; lateral lobes of peraeon segments separate, not contiguous or overlapping. Peraeon segments 5-7 with ventral adhesion spines.

Antenna 1 large, 4-segmented. Antenna 2 medium small, 4-segmented.

Mouthparts: Upper lip shallowly incised apically, lobes variously asymmetrical; epistome variously developed often strongly. Lower lip, inner lobes separated distally, small; outer lobes broad, moderately to widely separated. Mandible: molar flat, weakly triturative, with proximal molar seta; incisor typically 5-dentate; left lacinia basically 5-dentate,right lacinia trifid; blade spines present in spine row, Maxilla 1, body short, broad; outer plate with 6 (7) short apical spine-teeth; palp short, 1-segmented. Maxilla 2 short, outer plate distinctly set off from inner plate. Maxilliped: basal plates separated, segment 3 (ischium) not exceeding segment 2 (basis); palp 4-segmented, present in early life stages, often persisting in adult.

Gnathopod 1 medium, 6-segmented (ischium distinct); propodal palm distinct, dactyl short, with fused unguis; carpus large; basis slender. Gnathopod 2 large; 5-segmented (ischium fused with basis); propod elongate, palm oblique, bidentate; carpus small, cryptic; basis short, broad,with distinct anterior "flange":
Coxal gills usually simple, slender; accessory gills present, variously developed, 2-4 lobate.

Peraeopods 5-7 similar, 5-segmented; carpus large, propod large, elongate; dactyl large; merus small, subcryptic; ischium variously fused to short basis having large anterior flange.

Abdomen narrow. Male pleopods variously cleft distally, apices rounded, finely setulose.

Female: body size smaller and peraeon typically broader than in male; brood plates with marginal setae.

Remarks: As noted below, the percentage of species of the genus *Cyamus* (sens. lat.) remaining to be discovered is probably quite low. These cyamids tend to be ectoparasitic on large, relatively slow swimming and commercially important species of whales. Many thousands of whale carcasses have been examined and ectoparasites relatively frequently observed and collected during legal whaling operations that lasted for about two centuries.

Subgenus *Cyamus* Latreille, 1796
(revised status)

Type species: *Cyamus ceti* (L.) Lamarck, 1801
Species: *Cyamus erraticus* Roussel de Vauzème, 1834; *Cyamus gracilis* R. de Vauzème, 1834; *Cyamus ovalis* R. de Vauzème, 1834; *Cyamus monodontis* Lütken, 1873; *Cyamus nodosus* Lütken, 1873.

Diagnosis: Primitive cyamids, with generally plesiomorphic mouthparts and appendages.

Head elongate, lateral margins bulging posteriorly. Peraeon 2 slightly broadening posteriorly, hind corners produced. Peraeon segments 3 & 4 short, lateral "wings" separated. Peraeon segment 7 little broadening distally.

Mouthparts basic, little modified. Upper lip, epistome strongly developed. Lower lip, outer lobes large, narrowing distally. Left mandible, lacinia usually regularly 4-5-dentate; several blades in spine row. Maxilla 1, outer plate often with 7 teeth on left side, 6 on right side; inner distal margin bare. Maxilla 2, outer plate narrow, little exceeding inner plate. Maxilliped palp usually present in adult stage (except *C. gracilis*).

(continued on p. 71).

KEY TO GENERA OF CYAMIDAE

1. Peraeon 1 separated from head region [Figs. 1 (A.4); 27]; gnathopod 1 relatively large, palm vertical [Fig. 1 (F.1] . . . . 2.
Peraeon 1 distinctly fused with head [Fig 1 (A.1-3)]; gnathopod 1 relatively small, palm typically oblique or lacking [Fig. 1(F.2-4)] . . . . 3.

2. Peraeon 1 distinct from peraeon 2 [Fig. 26]; peraeon segments 6 & 7 distinct . ***Platycyamus*** (p. 102)
Peraeon segment 1 fused with peraeon 2, marked by marginal notch [Fig. 27]; peraeon segments 6 & 7 fused dorsally . . . . ***Syncyamus*** (p. 106)

3. Antenna 2 small, 4-segmented [Fig. 5A]; maxilla 2 inner & outer lobes distinct [Fig. 1 (D.1-3)] . . . . ***Cyamus*** (p. 65)
Antenna 2 minute, 2-3 (rarely 4) segmented [Fig. 24]; maxilla 2, inner lobe lacking [Fig. 1 (D.5)]. 4.

4. Coxal gills multi-branched [Fig. 23]; peraeopods 5-7 slender, segment 4 elongate [Fig. 1(H.1)]. . . . . ***Neocyamus*** (p. 101)
Coxal gills normal simple or paired [Figs. 2, 20]; peraeopods 5-7, stout, segments 4 short, ... [Fig. 1(H.2 -4)] . . . . 5.

5. Peraeon segments 6 & 7 separated dorsally [Fig. 9]; maxilliped 2-segmented [Fig. 1 (E.2-3)]. . . . 6.
Peraeon segments 6 & 7 fused dorsally [Figs. 27, 28]; maxilliped 1-segmented, fused basally [Fig. 1(E.4)] . . . .***Scutocyamus*** (p. 108)

6. Gnathopd 1, unguis of dactyl distinct [Figs 20, 24]; coxal gills single, with large accessory gill [Figs. .20, 21] . . . . ***Isocyamus*** (p. 96)
Gnathopod 1, unguis of dactyl fused [Fig. 2] ; coxal gills double, accessory gill lacking [Fig. 19] . . . . ***Orcinocyamus*** (p. 93)

KEY TO NORTH AMERICAN PACIFIC SPECIES OF *CYAMUS* (SENS. LAT.)

(not including *C. nodosus*, ectoparasitic on the Arctic narwhal, *Monodon monoceros*).

1. Outer plate of maxilla 1 typically with 6 apical spine teeth (occ. 7 on one , rarely on both), inner distal margin nearly bare [Fig. 7]; upper lip, epistome strongly developed distally [Fig. 5]. . . . . 1.
Outer plate of maxilla 1 usually with 7 apical spine teeth (both sides), inner distal margin strongly setose [Fig. 10]; upper lip, epistome weakly or not developed apically [Fig. 14]. . . . . 8.

2. Lower lip, outer lobes distally broad [Fig. 1(B.1)]; maxilliped palp usually lacking in adults [Fig. 1(E.3)] . . . . ***Cyamus (Paracyamus)*** 3.
Lower lip, outer lobes distally narrowing [Fig. 1 (B.2); maxilliped palp usually present in adults; [Fig. 1 (E.1)] . . . . **Cyamus *(Cyamus)*** 4.

3. Coxal gills very slender, elongate (both sexes) [Fig. 8]; antenna 1 elongate, >twice head length; peraeopods 5-7, segment 4 with acute posterior process; on *Megaptera novaeangliae*. . . . . ***C. (Paracyamus) boopis*** (p. 80)
Coxal gills relatively short, thick (sausage like in female) [Fig. 9]; antenna 1 short, < 2X length of head; peraeopods 5-7, segment 4 rounded below; on species of *Balaenoptera*. . . . . ***C. (Paracyamus) balaenopterae*** (p. 80)

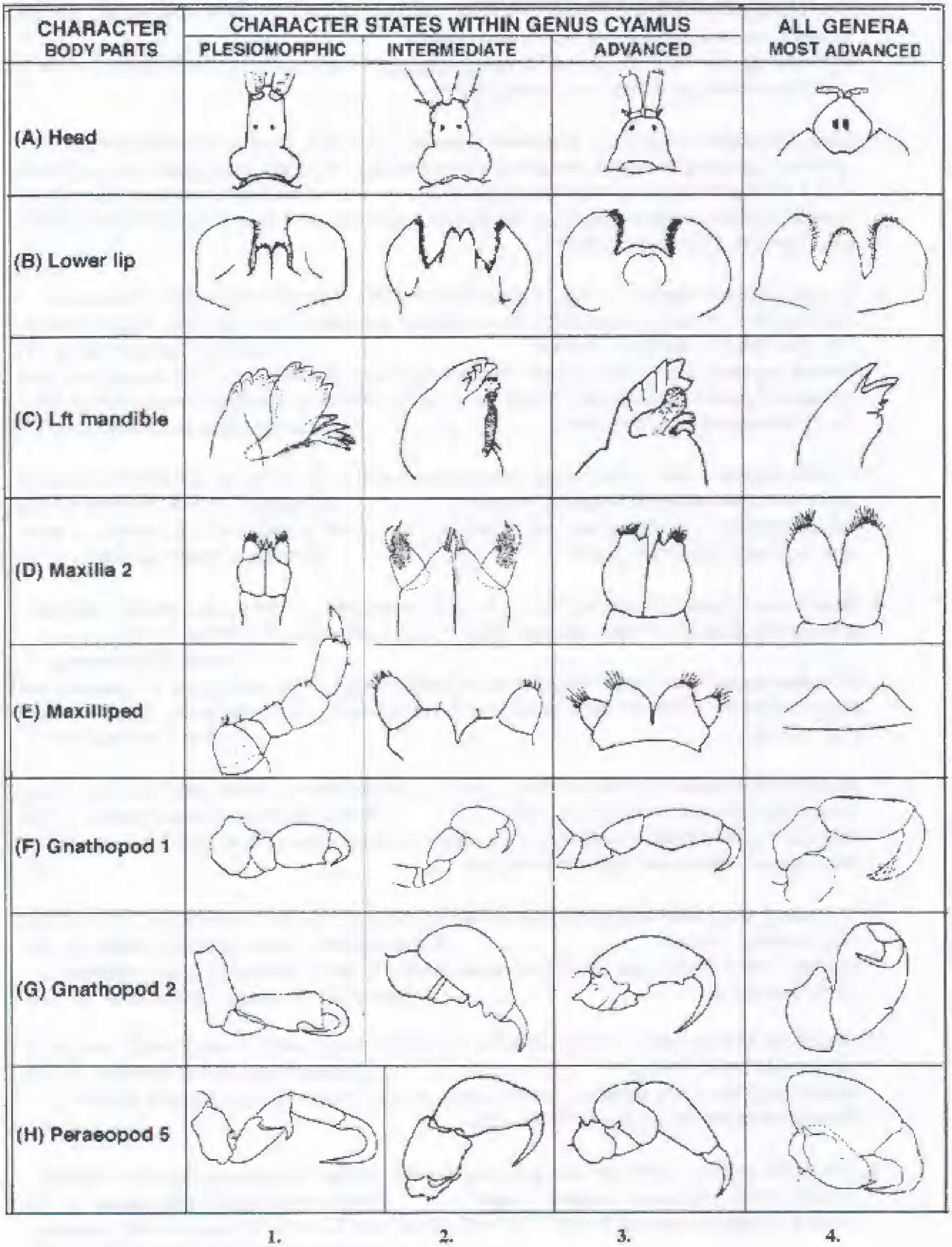

Fig. 1. Characters and character states within family Cyamidae.

4. Peraeon segment 5 & 6 with 2 pairs of ventral (adhesion) spines; maxilliped palp usually present in adults; on various Mysticeti and Monodontidae . . . . 5.
Peraeon segment 7 with single pair (or none) of ventral adhesion spines; maxilliped palp usually lacking in adults; on *Eubalaena glacialis* only . . . . 7.

5. Coxal gills double on each side of peraeon segments 3 & 4 [Fig. 5]; accessory gills elongate on peraeon 4; gnathopod 2, palm short, deeply concave [Fig. 1(G.1-2)]; maxilliped palp segments 2 & 3 subequal in length; on *Eubalaena glacialis* . . . . ***Cyamus (Cyamus) ovalis*** (p. 74)
Coxal gills single; accessory gills short; gnathopod 2, palm broad, shallow [Fig. 1(G.3)]; maxilliped palp, segment 2 less than segment 3 . . . . 6.

6. Peraeon segments narrow, "wings" widely separated [Fig. 3]; coxal gills slender, elongate, exceeding head; maxilla 2, outer plate large, distinctly exceeding inner plate [Fig. 3];on *Balaena mysticeta* and *Eschrichtius robustus*. . . . . ***Cyamus (Cyamus) ceti*** (p. 71)
Peraeon segments wide, "wings" narrowly separated; coxal gills relatively short, sausage-like, not extending beyond head; maxilla 2, outer plate narrow, little or not exceeding inner plate [Fig.4]; on *Delphinaptera* and *Monodon* . . . . ***Cyamus (Cyamus) monodontis*** (p. 71)

7. Peraeon segment 7 with 1 pair ventral (adhesion) spines [Fig. 6]; left mandible with 5-8 blades in spine row; accessory gills sexually dimorphic . . . . ***Cyamus (Cyamus) erraticus*** (p. 76)
Peraeon segment 7, ventral spines faint or lacking [Fig. 7]; left mandible with 2-3 blades in spine row; accessory gills small, similar . . . . ***Cyamus (Cyamus gracilis)*** (p. 76)

8. Head distinctly longer than broad [Fig. 1 (A.1-2)]; peraeopods 5-7 and dactyls powerful, elongate; gnathopod 2, propod powerful, elongate (Fig. 1(G.3)]; palms usually shallow, elongate. . . . . ***Cyamus (Mesocyamus)*** 9.
Head short, length little (or not) longer than basal width [Fig. 1(A.3)]; peraeopods 5-7, propods and dactyls relatively short and weak; gnathopod 2, propod short, deep, palm short, sharply concave [Fig. 1(G.2)] . . . . ***Cyamus (Apocyamus)*** 11.

9. Maxilliped palp usually present in adults; upper lip with moderate epistome; maxilla 2, inner plate exceeding outer plate; on *Physeter* only. . . . . ***Cyamus (Mesocyamus) catodontis*** (p. 82)
Maxilliped palp lacking in adults; upper lip, epistome indistinct or lacking; maxilla 2, outer plate the larger; on ziphiid and eschrichtiid whales. . . . . 10.

10. Antenna 1 large, much exceeding head; coxal gills slender, elongate, extending beyond head; on *Eschrichtius robustus* . . . . ***Cyamus (Mesocyamus) mesorubraedon*** (p. 87)
Antenna 1 short, little longer than head length; coxal gills short, not extending beyond head; on *Berardius bairdi* . . . . ***Cyamus (Mesocyamus) orubraedon*** (p. 84)

11. Maxilliped lacking palp in adults; lower lip, inner lobes nearly totally fused distally; maxilla 2, inner plate fused to outer . . . . ***Cyamus (Apocyamus) kessleri*** (p. 93)
Maxilliped palp usually present in adults; lower lip, inner lobes distally separated; maxilla 2, inner plate distinctly demarcated from outer. . . . . 12.

12. Coxal gills paired (double) on each side, strongly coiled [Fig. 13]; peraeon segment 2 broadly shield-shaped, with subacute lateral "wings" . . . . ***Cyamus (Apocyamus) scammoni*** (p. 90)
Coxal gills single, sausage-like [Fig. 15]; peraeon segment 2, lateral wings posteriorly broadest . . . . ***Cyamus (Apocyamus) eschrichtii*** (p. 90).

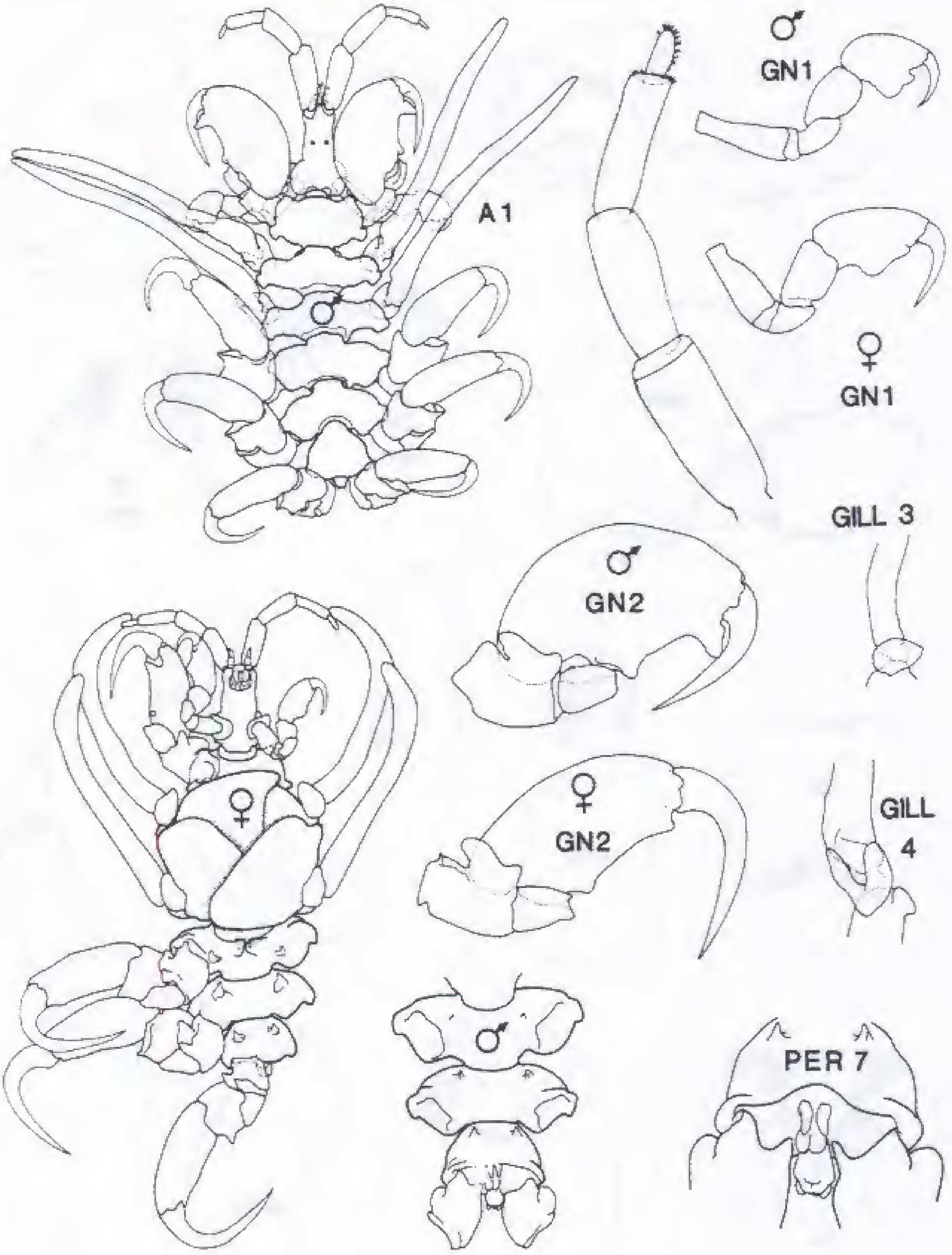

Fig. 2. ***Cyamus (Cyamus) ceti*** **(L.) Lamarck, 1801**. Male (12 mm); female (10.5 mm). ex *Balaena mysticetus*, Sooke, B. C.

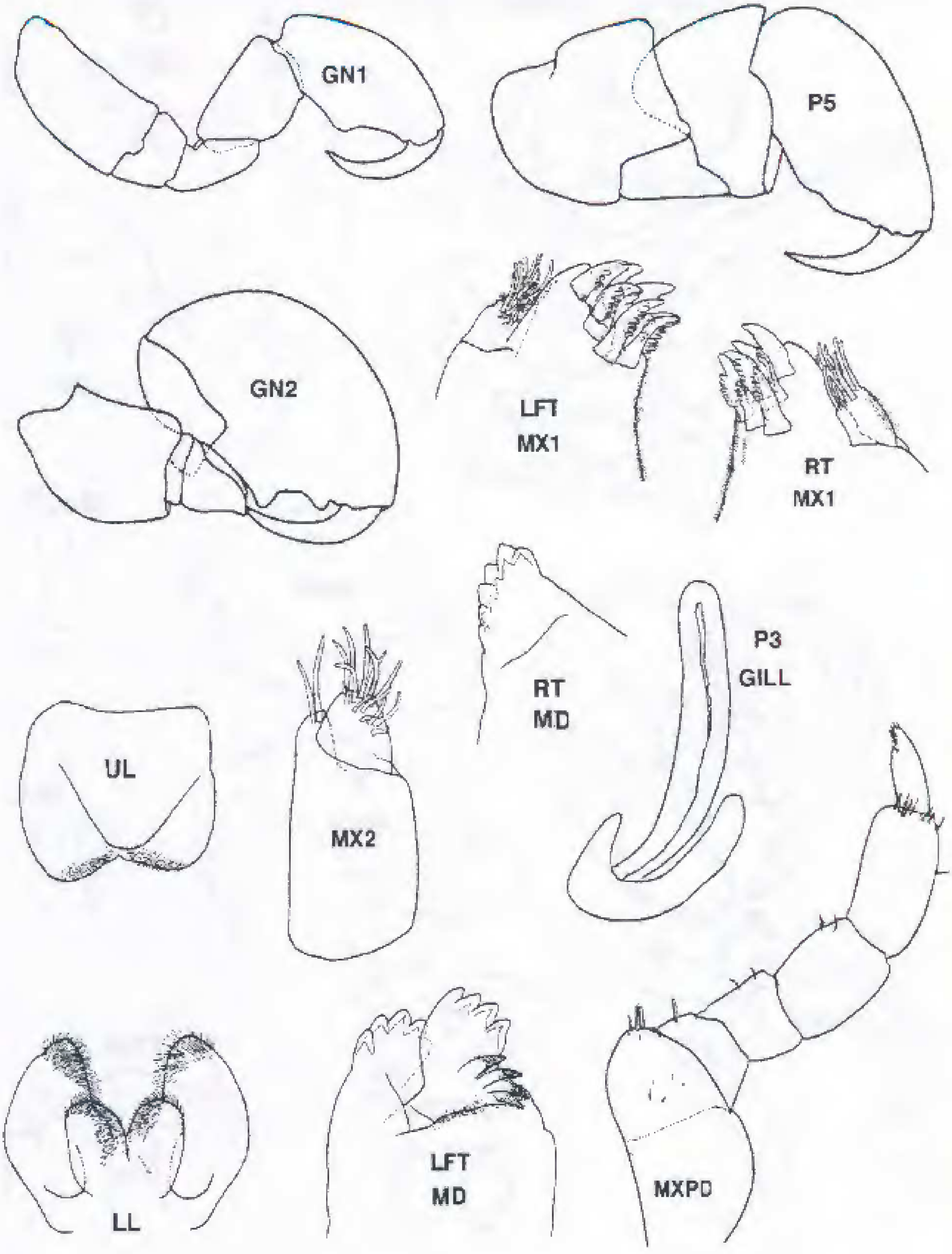

Fig. 3. ***Cyamus (Cyamus) ceti*** **(L.) Lamarck, 1801.** (peraeopods and mouthparts).

Gnathopod 1 distinctly 6-segmented, propod palm steeply oblique. Gnathopod 2 powerful, 5-segmented; anterior flange of basis strongly developed; propod powerfully elongate-ovate; dactyl strong. Peraeopods 5-7 powerful; carpus deep, propod elongate ovate; dactyl strong.

Coxal gills usually single, slender occasionally double on each side. Accessory gills double, variously developed.

Male pleopods deeply notched apically.

Female: generally smaller than male. Margins of brood lamellae strongly lined with setae.

Remarks: Most species of subgenus *Cyamus* are ectoparasites of primitive mysticetid whales (Balaenidae) but may occur also on *Eschrichtius*. Two species are apparently found only on arctic monodontid whales, a group that is not closely related to the Mysticeti.

Cyamus (Cyamus) ceti (L., 1758) (Lamarck, 1801)

(Figs. 2, 3)

Cyamus ceti Stephensen 1942; Margolis 1955; Leung 1967; Levin & Pfeiffer 1999.

Cyamus mysticeti Lütken, 1860; Lütken 1873.

Material Examined:

Sooke, B. C., ex stranded gray whale, Oct. 29/89, R. Baird & P. Steacy colls., - several specimens, CMN collections.

St. Lawrence Island, Bering Sea, Alaska, ex bowhead whale (*Balaena mysticeti*) -1 vial of specimens (identified for Bud Fay, June, 1961), CMN collections.

Point Hope, Alaska, ex. bowhead whale - 1 female specimen (identified for R. Rausch, February, 1963).

Alaska (loc. undet.), ex bowhead whale - 1 specimen (identified for Larry Jensen 16-IV-81), CMN collections.

Diagnosis: Male (to 12 mm)

Body short, broad; peraeon segment 4 widest; peraeon segments 5-7 each with single pair of ventral adhesion spines. Antennae typical of the genus.

Mouthparts: Upper lip broadly and shallowly notched below, lobes subequal. Lower lip, inner lobes distinct, mandibular lobes large, not widely separated Mandibular incisor appearing 4-toothed; left lacinia 5-dentate; 4 blades in spine row. Maxilla 1, outer plate with 7 apical spine-teeth on left side, 2 groups of 3 spines on the right; palp with stiff apical setae. Maxilla 2 short, small; inner plate small, with 1-2 apical setae; exceeded by distinct, broad, apically setose outer plate. Maxilliped palp distinct in adults; dactyl elongate, apex setulose (not subacute), inner margin not pectinate; segments 2 and 3 subequal in length; basis 1/2 fused to opposite number, lobe evanescent, margin with 2 setules.

Gnathopod 1 6-segmented, with slightly oblique propodal palm and dactyl lacking distinct unguis. Gnathopod 2 short, powerful, segments 3 & 5 vestigial; propod large, deep, palm steeply oblique, hinge tooth strong.

Coxal gills single, thick, with distinct, large, unequally paired basal accessory gills.

Peraeopods 5-7 short, powerful; basis short, broad, antero-distal flange large; segment 3 vestigial, partly fused to 2; segment 4 subcryptic, with no free anterior margin; segment 5 very short and deeper than length of basis; propod short, stout, with slight distal palm; dactyl short, not strongly curved.

Male pleopods regular. Penes nearly straight.

Female (ov.) (10.5 mm): brood lamellae large, margins strongly setose.

Remarks: Material illustrated here may vary slightly from that taken from arctic bowhead whales figured by Lütken (loc. cit.) and others.

Cyamus (Cyamus) monodontis Lütken, 1870.

(Fig. 4)

Cyamus monodontis Lütken 1873; Stephensen 1942; Leung 1967.

Material Examined:

Vancouver Public Aquarium, B. C., ex Beluga (*Delphinaptera leucas*), A. C. McNeill coll., November, 1972 - male (7.0 mm), slide mount, CMN NMCC 1989-101.

Diagnosis: Male (7.0 mm)

Body squat, medium broad, widest at peraeon segment 4. Peraeon segment 1 shield-shaped; peraeon segments 5-7 each with single pair of ventral spines.

Head markedly broadened at fusion of peraeon segment 1. Antenna 1 medium, little longer than head Antenna 2 normally 4-segmented.

Mouthparts: Upper lip with sharp distal notch, lobes subsymmetrical. Lower lip, outer lobes relative narrow, inner margins heavily setulose; inner lobes with shallow apical notch. Mandibular incisor unequally 5-toothed; left lacinia 5-6 dentate; right lacinia trifid, both with 3 thick blades in spine row. Maxilla 1 medium-large, deep, outer plate with 6 apical pectinate spine-teeth; palp relatively large, reaching end of outer plate, apex bearing several stout blade-like setae. Maxilla 2 very small; outer plate distinct, with several apical

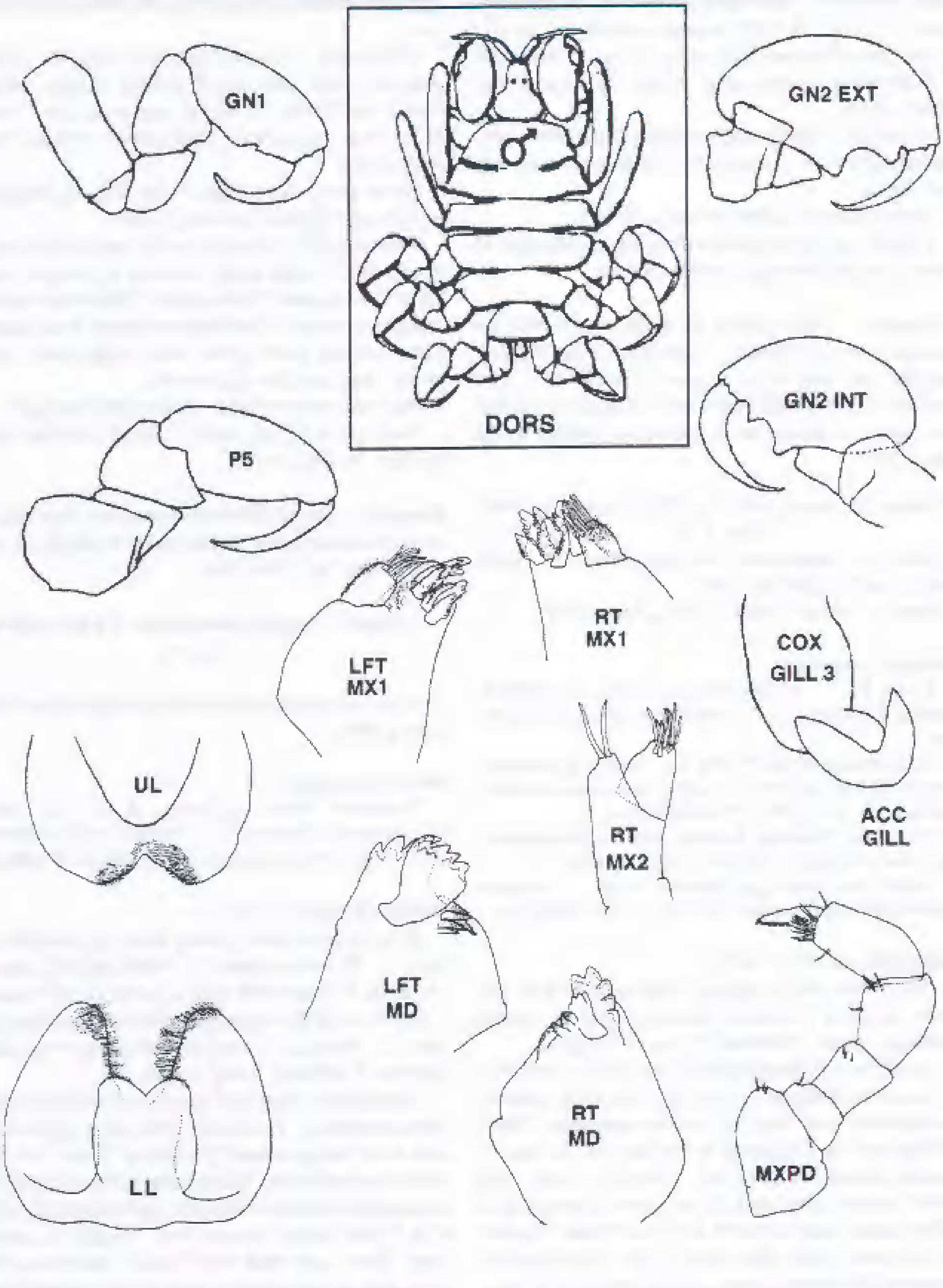

Fig. 4. *Cyamus (Cyamus) monodontis* **Lütken, 1873**. Male (7.0 mm) ex *Delphinaptera* (beluga). Vancouver Public Aquarium, B. C.

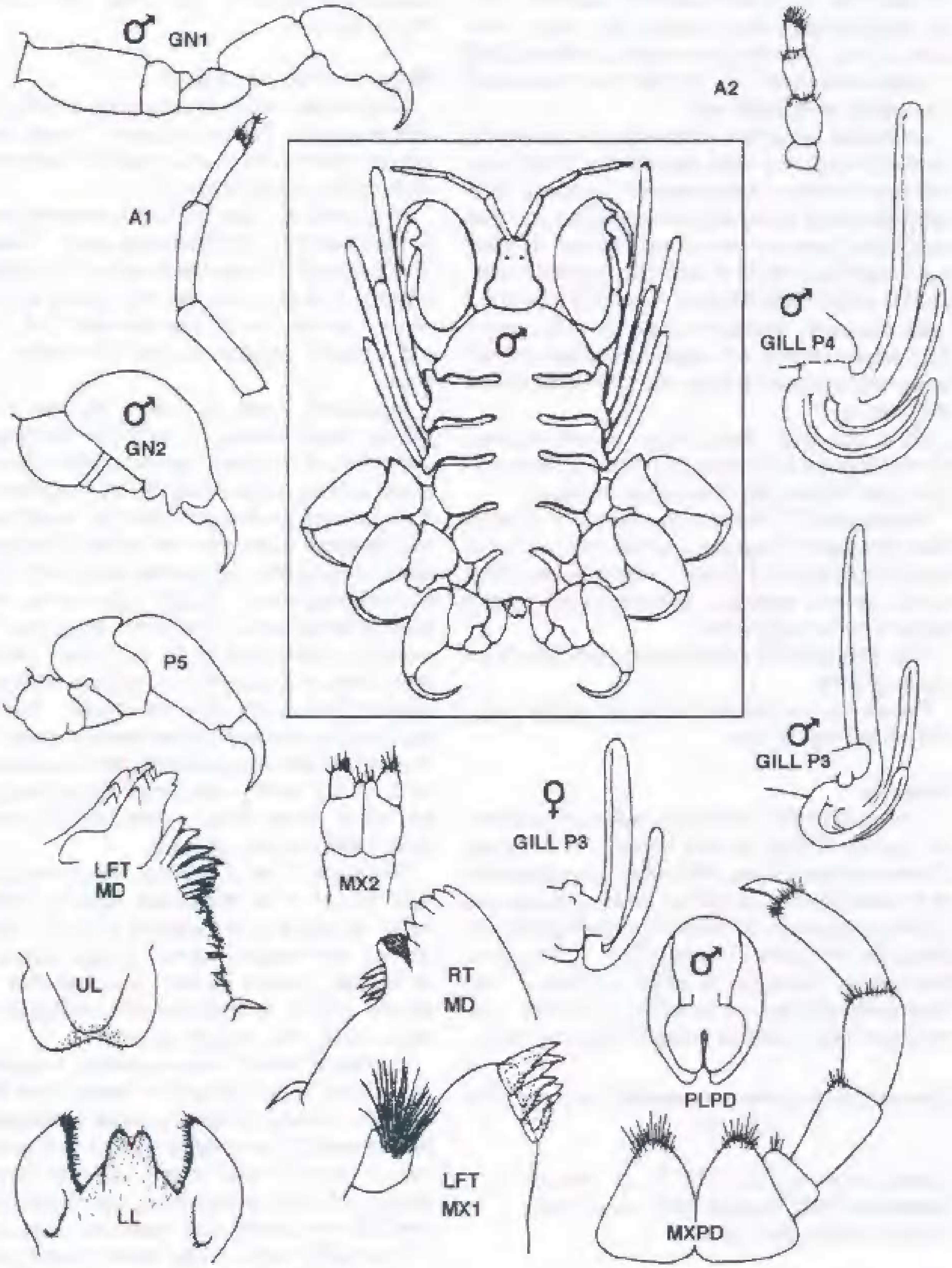

Fig. 5. ***Cyamus (Cyamus) ovalis*** **Roussel de Vauzème, 1834.** Male (16 mm); female (10 mm). ex *Eualaena glacialis*, North Pacific Ocean. (after Iwasa 1934; inset: after Lütken 1873).

setae, barely exceeding distinct inner plate tipped with 2-3 long setae. Maxilliped palp stout; segment 6 longest; dactyl medium-large, simple, apex acute; basal segment large, separated from opposing basis by half its length, lobe small with 2-3 short setae; segment 3, inner margin with single seta.

Gnathopod 1 relatively short; segment 3 narrowing anteriorly; segment 4 short; segment 5 short and deep, with short posterior margin; segment 6 medium, palm nearly horizontal, with small rounded tooth at proximal angle; dactyl strongly curved, unguis fused. Gnathopod 2, segment 2 very short and stout; segment 3 partly fused to antero-distal flange of segment 2; segment 4 small, triangular; segment 5 large, powerful, ovate, palm deeply concave, with stout sharp hinge tooth and strong tooth at posterior angle; dactyl medium, moderately curved.

Coxal gills large, thick, single on each segment, attached to peraeon via a short swollen stalk; accessory gills short, double, posterior slightly the larger.

Peraeopods 5-7 short, stout; segment 3 virtually fused to segment 2; segment 4 narrow, with short anterior margin; segment 5 short, with short acute hind margin; propod medium, narrowing distally; dactyl medium, not strongly curved.

Male pleopods with medium apical cleft cleft. Penes regular in form

Female (ov.) (to 6.0 mm?): brood lamellae ovate, with short marginal setae.

Remarks:

Cyamus (Cyamus) monodontis occurs on belugas in the northern Bering Sea and western Arctic Ocean. *Cyamus nodosus* Lütken, 1860, occurs more frequently on the arctic narwhal, and differs in having the dorsum of peraeon segments 3-7 divided into 2-4 rugged parts (Margolis 1954b, 1955; Leung 1967). *C. nodosus* is here assigned tentatively to subgenus *Cyamus*. The mouthparts have not yet been fully described. The maxilliped palp is lacking in adults (Margolis 1955).

Cyamus (Cyamus) ovalis Roussel de Vauzème, 1834

(Fig. 5)

Cyamus ovalis Lütken 1873; Iwasa 1934 (PL VI); Stephensen 1942; Margolis 1955; Leung 1967.
Cyamus tentator Dall, 1874.

Material Examined:

Off Alaska, southern Bering Sea, ex right whale - several male & female specimens (identified for D. Rice, Dec. 1964 & Jan. 1965, CMN collections.

Southern Bering Sea, ex right whale - several males & females (identified for D. Rice in Dec. 1964, Jan. 1965; CMN collections.

Diagnosis: Male (to 16 mm).

Body medium broad, widest at segments 3 & 4, lobes little separated. Peraeon segment 1 broad, anterior margin convex; peraeon segments 6 & 7 each with pair of obliquely set ventral spines.

Head medium long, sharply broadened at fused peraeon segment 1. Eyes subovate, black. Antenna 1 slender, elongate, 4-segmented, segments 1-3 subequal, segment 4 short, narrowing, with apical and lateral setae. Antenna 2 short, segments short, 2 & 3 larger and subequal, segment 4, apex subtruncate, short-setose.

Mouthparts: Upper lip narrow, shallowly notched apically, lobes subequal. Lower lip relatively narrow, outer lobes quite narrow, subacute; inner lobes fused except for sharp apical notch. Body of mandible short, stout; incisors 5-6 dentate; molar flat, weakly ridged, with proximal molar seta; left lacinia 5-dentate; 6-7 blades in spine row; right lacinia indistinctly trifid; 3-4 blades in spine row. Maxilla 1 short, broad, with six stout pectinate apical spine-teeth; palp short, thick, proximal, rounded apex with stiff setae. Maxilla 2 short, small, inner plate with 2-3 apical setae, distinctly exceeded by apically setose outer plate. Maxilliped palp large, present in adults; segment 6 longest, dactyl short, acute, inner margin strongly pectinate; basis (segment 2) large, totally separated from opposing member, apical (inner) plate rounded, setose, exceeding short, weakly setose segment 3.

Gnathopod 1 small, slender, 6-segmented; basis with trace of coxal attachment; segment 3 distinct, nearly as long as wide; segment 4 short, with short anterior free margin; segment 5 large, almost subrectangular; propod slightly larger, shallow, with sharply concave palm and broadly rounded posterior angle; dactyl short, slightly curved.

Gnathopod 2 short, stout, appearing 5-segmented; basis short, thick, with shallow antero-distal flange; segment 3 narrow, distinct; segment 4 subtriangular, lacking anterior free margin; segment 5 cryptic; segment 6 (propod) large, deeply subovate, narrowing distally, palm a short sharp notch, with strong hinge and proximal teeth; dactyl short, moderately curved.

Coxal gills medium long, slender, slightly exceeding head, unequally triple on peraeon 3, unequally quadruple on peraeon segment 4.

Peraeopods 5-7 short, stout, strong, 5-segmented, peraeopod 7 slightly smallest; segment 3 fused to short

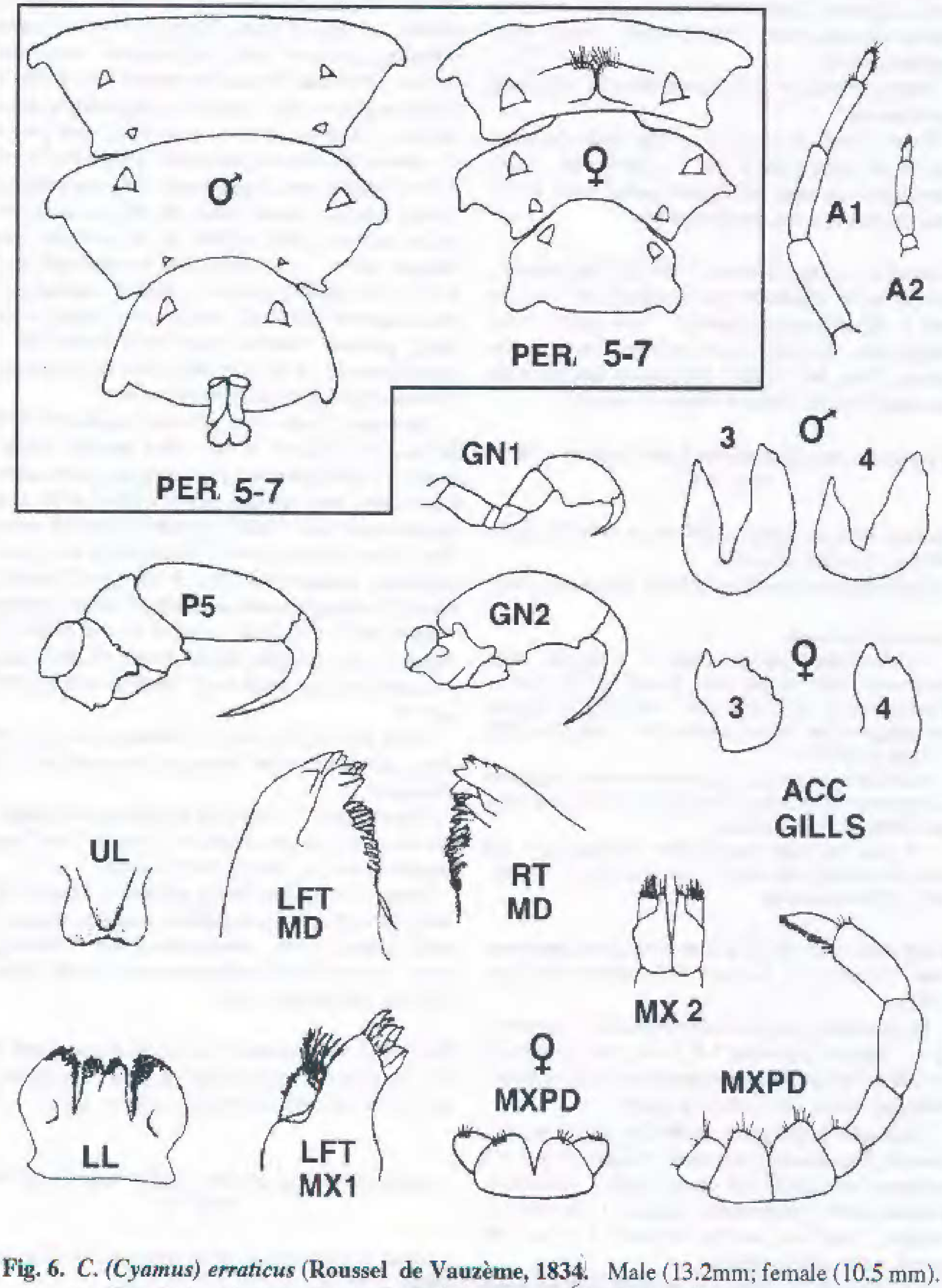

Fig. 6. ***C. (Cyamus) erraticus*** **(Roussel de Vauzème, 1834.** Male (13.2mm; female (10.5 mm). ex *Eubalaena glacialis*, Sooke, B. C. [after Iwasa 1934; Inset: after Margolis 1955).

basis having ventral facial adhesion spine; segment 4 small; segment 5, deep, hind margin short, toothed; propod elongate-ovate, palm indistinct; dactyl short, medium curved.

Fused pleopods of male incised laterally, with deep apical notch.

Female (ov.) (to 13.2 mm): Coxal gills unequally double on peraeopods 3 and 4. Gnathopod 2 with relatively broad palm and sharper palmar teeth. Brood lamellae large, ovate, margins setose.

Remarks: *Cyamus (Cyamus) ovalis* exhibits generally plesiomorphic character states, considerably more so than *C. (Apocyamus) scammoni*. The species is not uncommon, especially in the western North Pacific (Iwasa 1934) but, to date, the species has not been recorded from the coast of British Columbia.

Cyamus (Cyamus) erraticus R. de Vauzème, 1834

(Fig. 6)

Cyamus erraticus Lütken 1873; Iwasa 1934; Margolis 1955 (= *Cyamus glacialis*).
Paracyamus erraticus Barnard 1932; Stephensen 1942.

Material Examined:

Off west coast Vancouver Island, B. C., ex skin, black right whale (*Balaena glacialis*), landed at Coal Harbour Whaling Station, G. C. Pike coll. - ~40 males, 55 females, including juveniles of each (identified by Leo Margolis, Feb. 2, 1954, (PBS J2-54).

Southern Bering Sea, ex right whale (*Balaena glacialis*) - several males & females (identified for D. Rice, Dec. 1964; Jan. 1965), CMN collections.

Off Japan, ex 2 right whales (*Balaena glacialis*) - several males & females (identified for D. Rice, Dec. 1964; Jan. 1965, CMN collections.

Diagnosis: Male (to 13.2 mm, or larger in specimens from Atlantic and southern hemisphere (Margolis, 1955).

Body medium large, broadest at peraeon segments 3 & 4. Peraeon segments 5 & 6 each with 2 pairs of ventral spines (anterior pair larger); peraeon segment 7 with one pair of stout adhesion spines.

Head medium longer, expanded basally. Antenna 1 slender, 4-segmented, segments subequal; segment 4 subacute, with apical and lateral setules. Antenna 2, medium-short, 4-segmented; segment 1 very short, 3 longest, 2 medium, swollen; segment 4 acute, with apical and marginal setules.

Mouthparts: Upper lip narrow, with shallow apical notch; lobes subequal; epistome prominent. Lower lip, outer lobes narrow, inner margins straight; inner lobes tall, apically sharply separated. Mandibular incisor 5-dentate; left lacinia large, 5-dentate, with 6-7 blades extending alongside molar; right lacinia narrow, tridentate, with distal flat process; several short blades in spine row proximally; molar flat, with proximal plumose seta. Maxilla 1 narrow, apex with 6 stout pectinate spine-teeth; palp set proximally, longer than wide, with numerous strong apical setae, and outer marginal setules. Maxilla 2 small, inner lobe distinct, apex with two setae; outer plate distinct, narrow, truncate apex strongly setose. Maxilliped palp 4-segmented, relatively stout, usually present in adults, especially female; segment 6 distinctly longest, dactyl strong, acute, finely pectinate distally; basis fused proximally to opposite number, lobe prominent, distally setulose, not exceeded by distally setulose segment 3.

Gnathopod 1 small, 6-segmented; segment 3 small but distinct; segment 4 with short anterior margin; segment 5 subrectangular; segment 6 (propod) expanding distally, palm straight, nearly vertical, with small median tooth and sharply rounded proximal angle; dactyl short, slightly curved. Gnathopod 2 short, stout, appearing 4-segmented (3 fused with 2 and 5 cryptic); basis with strong bifurcate anterodistal flange; segment 4 short, with short distal process; propod shallowly subovate, palm medium, shallowly concave, both hinge tooth and proximal tooth weak; dactyl medium, gently curved.

Coxal gills single, slender, elongate; accessory gills short, paired, posterior longer, apices acute, sexually dimorphic.

Peraeopods 5-7 very short, stout;segment 4 lacking anterior free margin; segment 5 deeper than long; propod narrowing distally; dactyl strong

Female: (ov.)(to 10.5 mm): peraeon segments 5 & 7 with 1 pair of stout ventral adhesion spines; peraeon 6 with 2 pairs of spines, anterior pair larger. Coxal gills each with single irregularly lobate accessory gill. Brood lamellae marginally setose.

Remarks: *C. (Cyamus) erraticus* is distinguished by the two pairs of ventral spines on peraeon segment 6, and by the sexually dimorphic accessory gills.

Cyamus (Cyamus) gracilis R. de Vauzème, 1834

(Fig. 7)

Cyamus gracilis Lütken 1873; Margolis 1955; Leung 1967.
Paracyamus gracilis Barnard 1932.

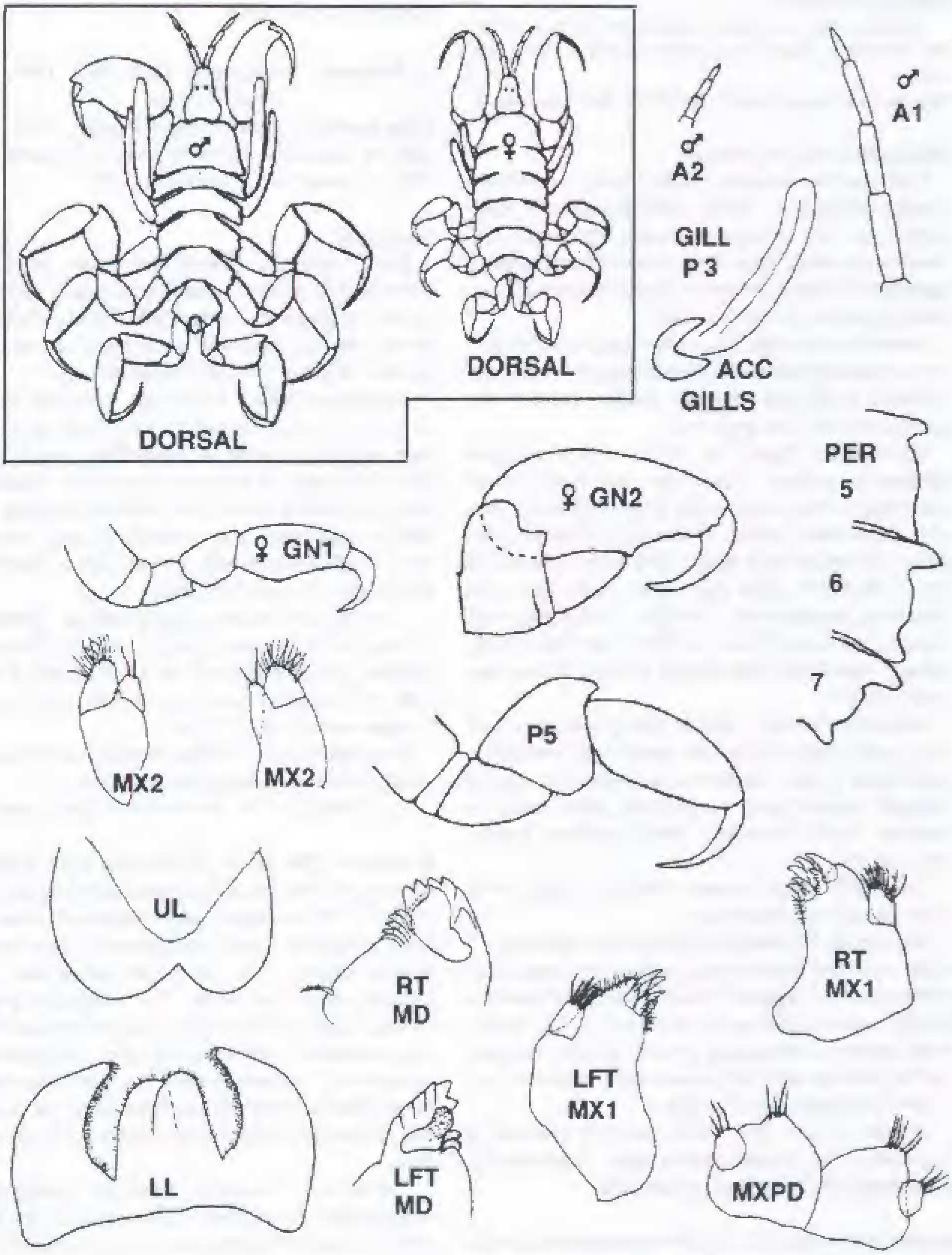

Fig. 7. *Cyamus (Cyamus) gracilis* **(R. de Vauzème).** Male (10 mm); Female (ov.) (8 mm), ex *Eubalaena glacialis*, North Pacific Ocean [after Iwasa (1934); Inset: after Lütken (1873)].

Material Examined:

Victoria, Mass., USA, ex northern right whale, Rowntree coll., 29/09/86. Male, female slide mounts, CMN collections.

Original material ex southern right whale, *Balaena australis*.

Diagnosis: Male (to 10 mm).

Head narrow, elongate, slightly widening at fused peraeon segment 1. Body relatively slender, long-ovate in outline; broadest at peraeon segments 3 & 4. Peraeon segment 2 large, deep, shield-shaped; peraeon segments 5-7 lobate laterally, sloped posteriorly, each with single pair of ventral spines.

Antenna 1 relatively short, little longer than head, 4-segmented; segments 1-3 subequal; segment 4 slender, relatively long, apex subacute, weakly setose. Antenna 2 medium, 4-segmented.

Mouthparts: Upper lip, lobes subsymmetrical, epistome prominent. Lower lip, outer lobes sharply narrowing distally, inner lobes deeply separated apically. Mandibular incisor 6-dentate; left lacinia scabrous; right lacinia with single large tooth; 2 blades in left, 5 blades in right spine row; molar flat, with prominent proximal seta. Maxilla 1, outer plate with 6 spine-teeth on each side. Maxilla 2, outer plate large, setose. Maxilliped palp lacking in adult stages; segment 3 small.

Gnathopod 1 small, slender, 6-segmented; propod ovate, palm oblique, proximal tooth weak, rounded. Gnathopod 2 short, appearing 4-segmented; propod elongate, shallow, narrowing distally; palm shallowly concave, nearly horizontal; dactyl medium, moderately curved.

Coxal gills single, slender, medium length, with short subequal accessory gills.

Peraeopods 5-7 slender, medium long; peraeopod 7 slightly shortest; basis slender, lacking processes, fused with segment 3; segment 4 small, lacking free anterior margin; segment 5 (carpus) very large, long, anterodistal process overhanging propod; propod elongate, shallow, narrowing distally; dactyl long, gently curved.

Male pleopods as in *C. ovalis*.

Female (ov.)(to 10.0 mm): peraeon broadest at segments 4 & 5, broader than in male. Gnathopod 2, propod apparently lacking palmar teeth.

Remarks: *Cyamus (C.) gracilis* is ectoparasitic on the northern right whale but has seldom been recorded from the North Pacific region, and not to date from the North American sector.

Subgenus *Paracyamus* G. O. Sars, 1895, revived status

Type Species : *Cyamus boopis* Lütken, 1870

Species: *Cyamus balaenopterae* K. H. Barnard, 1931; *Cyamus pacifica* Lütken, 1873.

Diagnosis:

Head, elongate, sharply broadened posteriorly. Peraeon 2-4, segments narrow, distinctly separated. Peraeon segment 2 subrectangular, hind corners produced. Peraeon segments 5-6 with paired ventral spines; peraeon segment 7 broadened posteriorly.

Mouthparts basic. Upper lip, epistome strongly developed. Lower lip, outer lobes broad, inner lobes short, deeply separated. Left mandible, lacinia irregularly 4-5-dentate; 2-4 blades in spine row. Maxilla 1, outer plate with 6 apical spine- teeth on each side, inner distal margin nearly bare. Maxilla 2, outer plate relatively small, little exceeding inner plate. Maxilliped, palp usually lost in adult stage.

Gnathopod 1, palm regularly oblique. Gnathopod 2 stout, 4-5 segmented; propod medium deep, palm shallow, nearly horizontal, dactyl medium. Peraeopods 5-7 strongly developed; carpus deep; propod elongate-ovate, dactyl strong.

Coxal gills single, medium, slender. Accessory gills small, paired and subequal on each side.

Male pleopods with medium deep distal notch.

Remarks: The genus *Paracyamus* Sars, 1895 was submerged within the genus *Cyamus* by Margolis (1955, 1959). The maxilliped palp is retained in the adult stage of most members of subgenus *Cyamus*, but lost in most species of the other three subgenera. This character state alone is therefore insufficient grounds for subgeneric, let alone full generic recognition. However, consistent differences in other mouthparts and general body features noted above, and in the key (p. 66) are here considered reasonable bases for resurrection of a modified subgeneric concept of *Paracyamus* Sars.

The status of *Cyamus (P.) pacifica* Lütken and its cetacean host is uncertain. This ectoparasite has apparently not been recorded from the northeastern Pacific region.

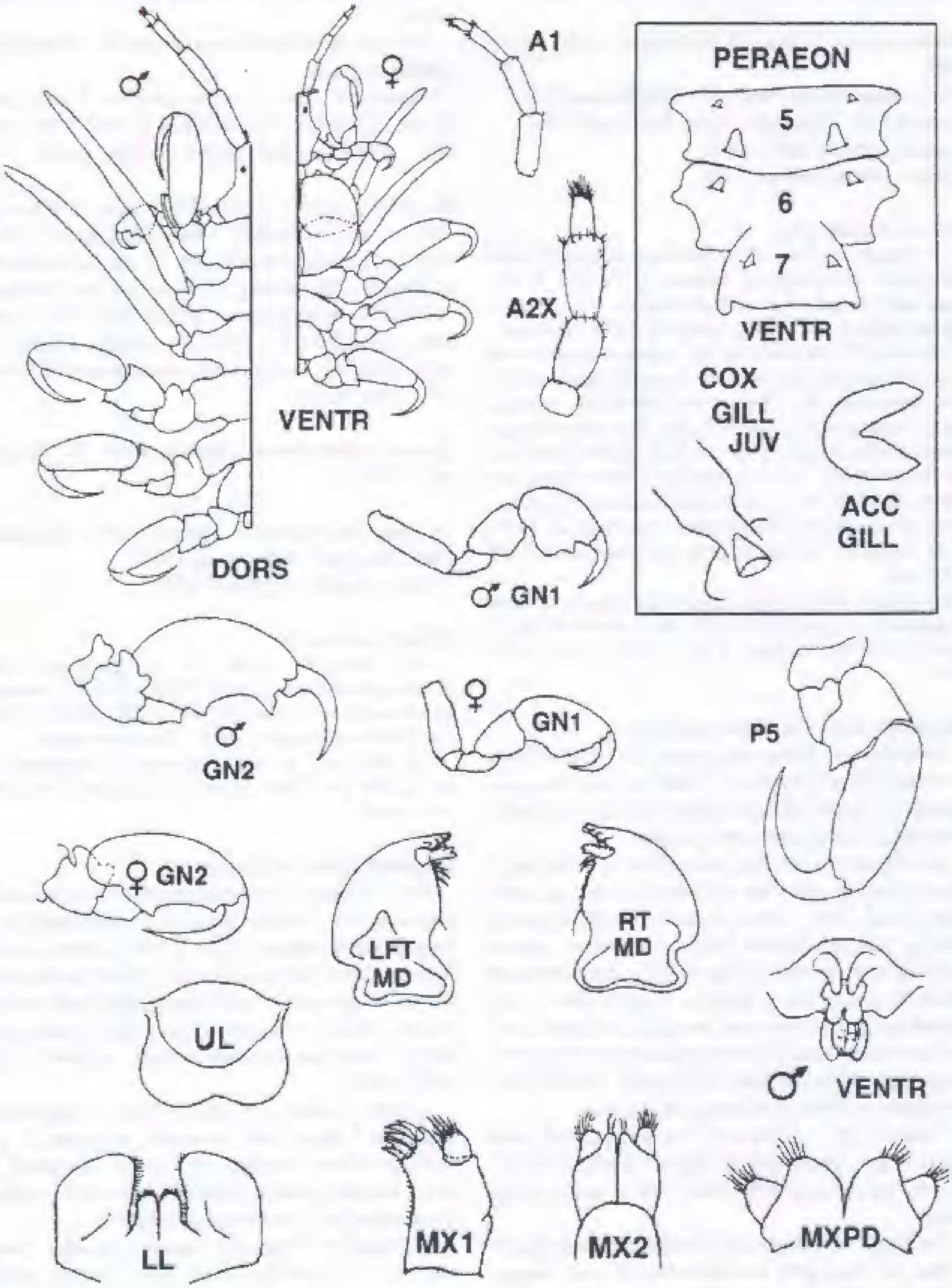

Fig. 8. ***Cyamus (Paracyamus) boopis* Lütken, 1870.** Male (12 mm); female (ov.) (7.2 mm). ex *Megaptera novaeangliae*. North Pacific Ocean (after Sars 1895; inset: after Margolis 1955).

Cyamus (Paracyamus) boopis Lütken, 1870

(Fig. 8)

Cyamus boopis Lütken 1873; Margolis 1955; Leung 1967.
Paracyamus boopis Sars 1895; Stephensen 1942; Barnard 1932; Margolis 1954a; Rowntree 1996.
Cyamus suffusus Dall, 1872a.
Cyamus elongatus Hiro, 1938.

Material Examined:

Off Vancouver Island, B.C.: ex skin of humpback whale (*Megaptera novaeangliae*), summer, 1952, PBS J7-53 - many male, female & juvenile specimens (3 males and 3 females studied, slide mounts prepared, CMN collections.

60 miles NE of Hawke's Island, Labrador, western North Atlantic Ocean, ex skin, humpback whale *Megaptera nodosa* R. L. Stevenson coll., 1 Sept., 1950, PBS B5-55 - 3 mature males, 2 young males, 1 mature female, 2 immature females [forwarded by Dr. D. E. Sergeant, FRB], CMN collections. Off South Africa? , ex skin, humpback whale *Megaptera nodosa* PBS B29-54 - 9 mature males, 2 mature females, 4 immature female [sent from South African Museum by Dr. K. H. Barnard, 28 April, 1954; no other data], CMN collections.

Tonga Island, South Pacific Ocean, ex humpback whale *Megaptera novaeangliae*, PBS B9-64 - 6 specimens [rec'd from Dr. Yuk-maan Leung, Aug.24, 1964], CMN collections.

Diagnosis: Male (to 12 mm. or larger).

Body slender. Peraeon segments 5-7 each with pair of ventral adhesion spines. Head slender, elongate. Antenna 1 slender, elongate, segments 1 & 2 subequal; Antenna 2, regular, segment 3 longest.

Mouthparts: Upper lip with shallow median notch, lobes subequal, epistome moderate. Lower lip, outer lobes broad, inner lobes narrow, deeply separated distally. Mandibular left lacinia 4-5-dentate, with 4 proximal blades; right lacinia trifid, with 2 proximal blades in spine row. Maxilla 2 small, inner lobe distinct, apically short setose, exceeded by distinct setose outer lobe. Maxilliped palp lacking in adult specimens (Sars 1895; Margolis 1955); basis weakly fused to opposite number, lobe marginally setose.

Gnathopod 1, segment 3 distinct; propod deep, palm oblique. Gnathopod 2, segment 2 with large anterior flange; propod with small palmar teeth; dactyl short.

Coxal gills single, slender, elongate; accessory gills at base of coxal gills are spine-like in early stages, subequally bifurcate in adult males and females [no ventral spines present (see Margolis 1955)].

Peraeopod 5-7 stout, 5-segmented. Basis short; propod elongate-ovate, lacking palm; dactyl strongly curved.

Male pleopods deeply notched distally. Penes short, curved medially.

Female (ov.) (to 7.2 mm+): peraeon 5 with 2 pairs of ventral adhesion spines, 1 pair on each of peraeon 6 & 7. Brood lamellae regular, margins setose.

Remarks: *Cyamus (C.) boopis* is apparently host specific to the humpback whale (*Megaptera novaeangliae*). Maxilliped palps are present in juveniles (to ~6 mm) but are lacking in mature females of Atlantic and Pacific populations. The description of *Cyamus elongatus* Hiro, 1938, from the western Pacific, was apparently based on juvenile specimens of *C. boopis* (Margolis 1955).

Cyamus (Paracyamus) balaenopterae K. H. Barnard, 1931.

(Fig. 9)

Cyamus balaenopterae Barnard 1932; Stephensen 1942; Margolis 1959; Leung 1967.
Cyamus pacificus Lütken, 1873?

Material Examined:

Off Vancouver Island, B. C., ex minke whale (*Balaenoptera acutorostrata*), 1955? - 5 male, 4 immature female speci-mens (identified for G. Clifford Carl, February, 1956 (see Margolis, 1959), CMN collections.

Off California, ex skin of blue whale; 2 specimens (identified for Dale Rice, February, and April, 1964, CMN collections.

Diagnosis: Male (to 5.0 mm).

Body slender to medium-broad, widest at peraeon segments 4-5. Peraeon segment 2 subrectangular, not deep; peraeon segments 3 & 4, lobes narrow, moderately separated; peraeon segment 7 distally subtruncate. Peraeon segments 5-7 each with single pair of stout ventral (adhesion) spines. Head elongate, posteriorly sharply broadened at fused peraeon segment 1; eyes small, round.

Antenna 1 relatively short and stout, 4-segmented; segments 1 larger than subequal segments 2 & 3; segment 4 short, rounded, with apical and lateral setules. Antenna 2 small, segment 1 very short, 3 longest, 2 not broadened, 4 with apical setal tuft.

Mouthparts: Upper lip narrow, apically sharply notched. Lower lip, outer lobes narrow, sharply rounded, with strong inner distal setules; inner lobes, low, deeply separated. Mandibular incisor 4-5 dentate; molar flat, weakly triturative and setulose, with

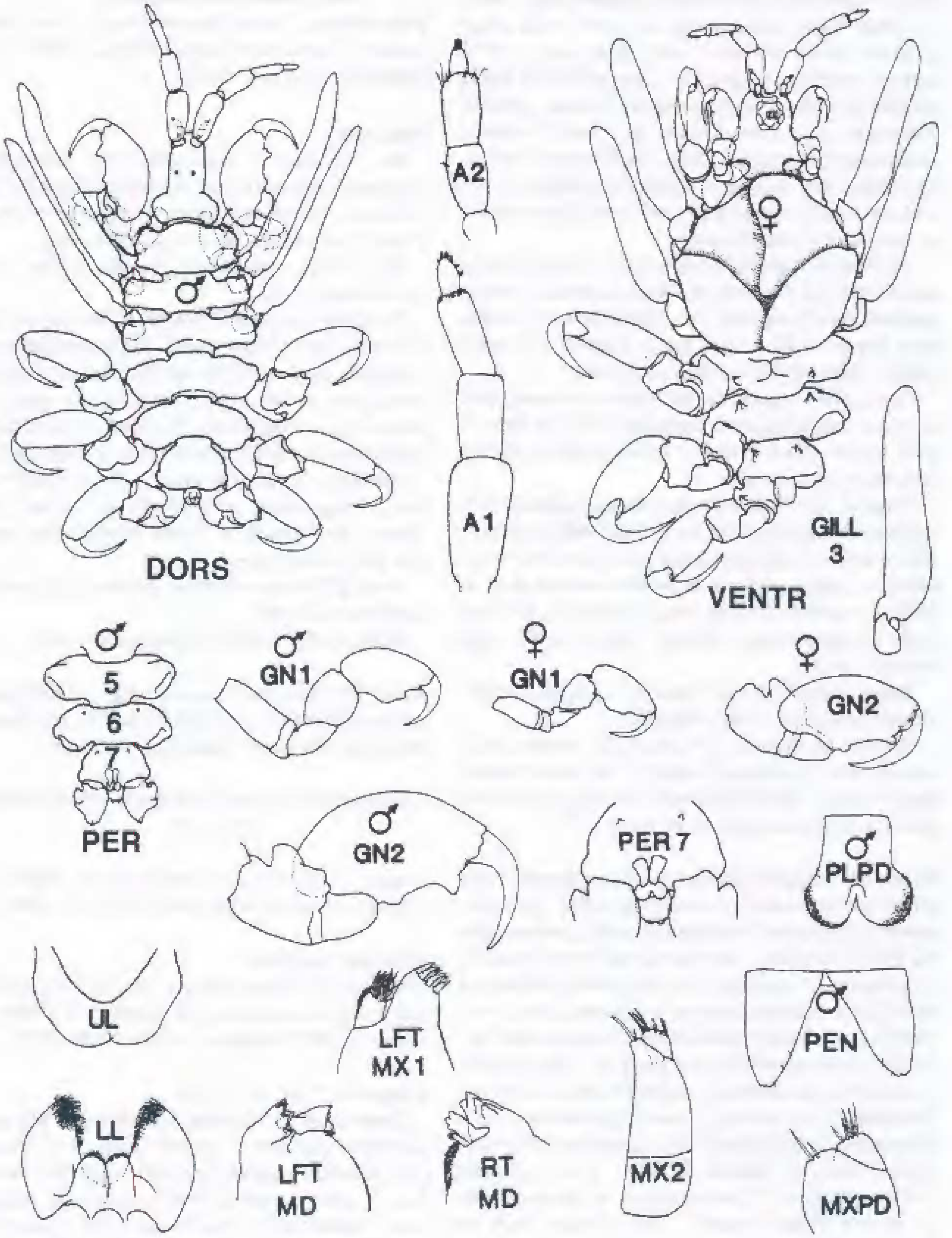

Fig. 9. ***Cyamus (Paracyamus) balaenopterae*** **Barnard, 1931.** Male (5.0 mm); female (4.2 mm), ex *Balaenoptera acutirostrata*, off Vancouver I., B. C.

thin proximal seta; left lacinia tridentate, with 1 short proximal blade; right lacinia tricuspate, with single proximal blade. Maxilla 1 short, stout, apex with 6 longish pectinate spine-teeth; palp relatively large, proximally with numerous strong apical setae. Maxilla 2 medium, inner lobe distinct, apex with 2 unequal setae; outer plate small, distinct, apically weakly setose. Maxilliped palp lacking in adults; basis medium, lobe shallow, weakly setose; segment 3 small, little exceeding seg-ment 2, margin setose.

Gnathopod 1 small, 6-segmented; propodal palm steeply oblique. Gnathopod 2 large, essentially 4-segmented, narrow segment 3 is anteriorly fused within large flange of short stout basis; segment 4 rounded behind; segment 6 large, deep, subovate;

Coxal gills elongate slender, single; accessory gills elongate (not triangular), unequally bifid at base of each gill (in male), posterior lobe extending slightly beyond peraeon margin.

Peraeopods 5-7 short, stout, subequal, essentially 5-segmented, segment 3 anteriorly fused with short basis that bears a small anterior flange and sharp inner facial adhesion spine; segment 4, anterior margin short or lacking; segment 5 large, deep; segment 6 (propod) large, elongate-ovate, lacking palm; dactyl large strongly curved.

Male pleopods deeply separated apically. Penes, broadly triangular, nearly straight.

Female (ov.) (to 4.2 mm): coxal gills shorter, more sausage-like; gnathopods smaller and more slender than in male. Brood lamellae form large subcircular pouch, margins strongly short-setose.

Remarks: Margolis (1959) could detect no noticeable difference between his material from a B. C. sei whale and that from a South African blue whale, on loan from the British Museum. Despite general host specificity of cyamids, *C. balaenopterae* has been identified on blue, fin, and minke whales, suggesting little or no modification during evolution of present rorqual species from a presumed common ancestor. This phenomenon may be attributable to hybridization of blue and fin whales that apparently occurs at greater frequency than among other Mysticeti, and is geographically widespread (Berta & Sumich 1999). Thus, Margolis (1959) anticipated *C. balaenoptera* to be found also on Sei and Bryde's whales. This surmise might be carefully checked by re-examination of ectoparasites from all five rorqual species that occur commonly along the B. C. coast.

Mesocyamus, new subgenus

Type species: *Cyamus mesorubraedon* new species. Species: *Cyamus orubraedon* Waller, 1989; *Cyamus catodontis* Margolis, 1954a.

Diagnosis:

Body medium to large. Peraeon segment 2 subrectangular, corners lobate. Peraeon segments 5-7 each with a pair of well-developed ventral spines. Peraeon 7 hour-glass shaped, broadening posteriorly.

Head medium, posteriorly strongly bulging. Antennae medium strong.

Mouthparts regular. Upper lip with weak epi- stom. Lower lip, outer lobes broad. Left mandible, lacinia irregularly dentate; 0-3 blades in spine row; Maxilla 1, outer plate usually with 7 apical spine-teeth; inner distal margin finely setose. Maxilla 2, outer plate large. Maxilliped trending to loss of palp in adult stage.

Gnathopod 1, palm toothed, oblique. Gnathopod 2 stout, 4-segmented, propod elongate-ovate, dactyl strong. Peraeopods 5-7 stout, carpus broad, propod and dactyl long, strong.

Coxal gills single, slender. Accessory gills medium, paired on each side.

Male pleopods, distal notch medium deep.

Remarks: The known species within this subgenus are ectoparasites of advanced Mysticeti (*Eschrichtius*) and primitive Odontoceti (Ziphiidae, *Physeter*).

Cyamus (Mesocyamus) catodontis Margolis, 1954a
(Fig. 10)

Cyamus boopis var. *physeteris* Pouchet, 1888.
Cyamus catodontis Margolis 1955; Leung 1967.

Material examined:

Type lots: ex *Physeter macrocephalus* (Margolis original description, loc cit.); slide mount (ELB-EAH prep.), August, 2000 (**Paratype**). CMNC 2000-0003.

Diagnosis: Male (to 7.2 mm)

Body short, broadening posteriorly to segment 5; peraeopod segment 2 subrectangular, 3 & 4 narrow, lobes laterally separated; segment 6 slightly narrower than 5; lobes curved (arched) posteriorly; peraeon 7 broad subtriangular, hind margin gently convex; ventral surface of 6-7 each with single pair of stout adhesion spines.

Antenna 1 strong, segment 1 thickest; segment 2

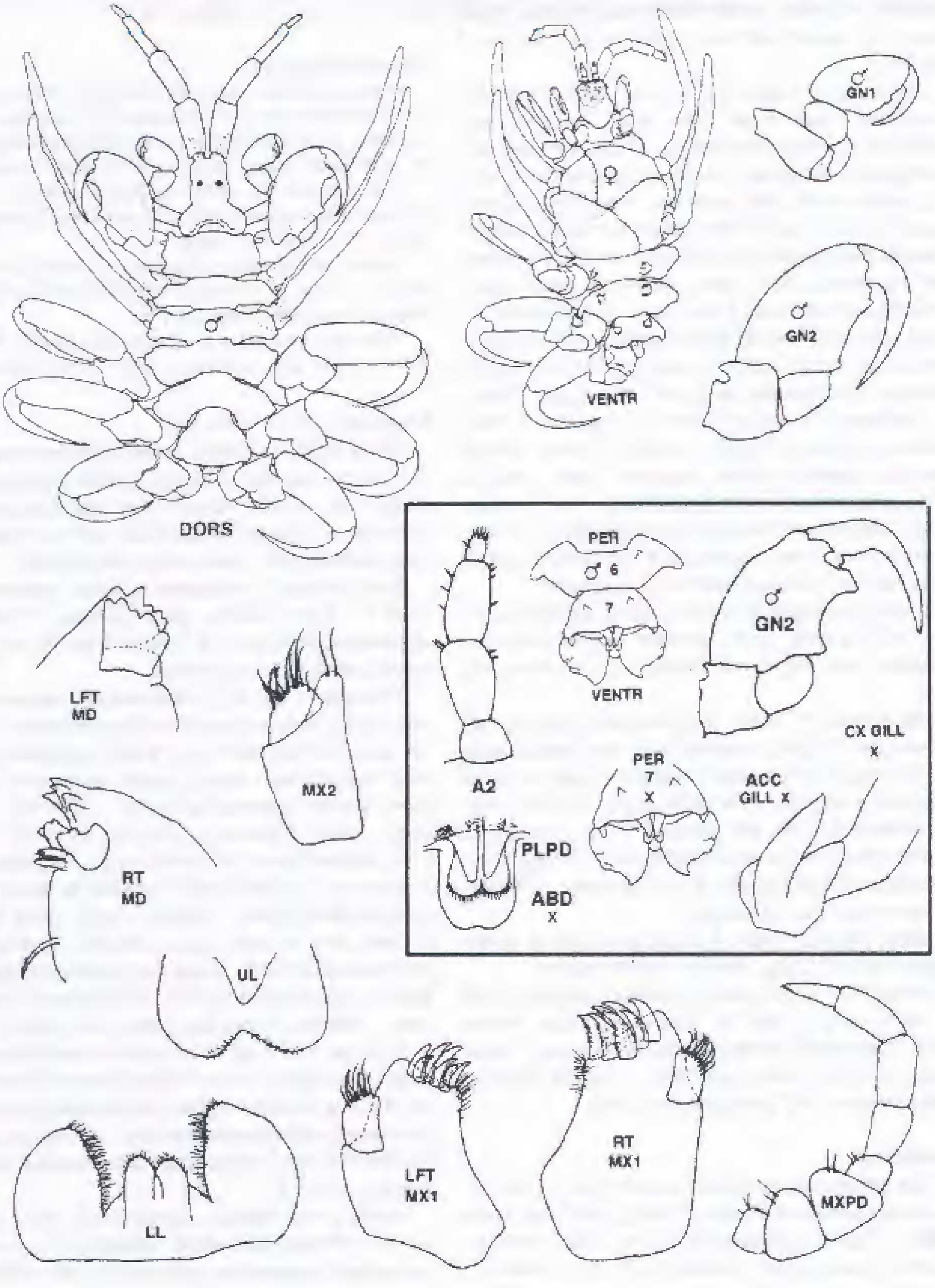

Fig. 10. ***Cyamus (Mesocyamus) catodontis*** **Margolis, 1954.** Male (Holotype) (7.2 mm); female (allotype) (5.9 mm); ex *Physeter macrocephalus* (Inset: after Margolis 1954a).

thinner, subequal in length; segment 3 slender, shorter; segment 4 slender, with lateral marginal and apical setae. Antenna 2 very short, 4-segmented, segment 4 distinct.

Mouthparts: Upper lip weakly incised apically. Lower lip , outer lobes broad, inner margin setose. Mandibular incisor appearing 4-5 dentate (tridendate in original description). Maxilla 1, palp medium, apically setose; outer plate apparently with 7 apical pectinate spine-teeth, and finely setose inner distal margin. Maxilla 2, outer plate small but distinct, apically setose, not exceeding inner plate, having 2 apical setae. Maxilliped palp usually (but not always) present in adult male and female; basis nearly completely separated from opposite member; segment 3 small, weakly setulose, not exceeding marginally setose lobe of basis.

Gnathopod 1 medium small, 6-segmented; basis slender; segment 3 narrow, lacking distinct anterior margin; segment 4 short; segment 5 short, medium deep; propod deep-ovate; palm oblique, with medium hinge tooth remote from base of regular dactyl. Gnathopod 2 short, stout, appearing 4-segmented; propod deep, palmar and hinge teeth well developed.

Coxal gills single, medium-elongate, slender; accessory gills paired, short, subequal, apices subacute, posterior lobe slightly the larger; palm medium convex.

Peraeopods 5-7 short, very powerful, 5-segmented; peraeopod 7 slightly shortest; basis very short, broad, with strong curved anterior marginal cusp and stout adhesion tooth at posterior angle; segment 4 small, with no anterior free margin; segment 5 large, deep, with antero-distal process overhanging base of large, elongate propod, lacking palm; dactyl very large, powerful, very strongly curved (arched).

Male pleopods with medium deep apical notch. Penes relatively long, slender, slightly curved.

Female (ov.)(to 5.9 mm): peraeon segments 5, 6, & 7) each have 1 pair of ventral adhesion spines. Maxilliped palp frequently lacking in adult stage. Coxal gills relatively short and thick. Brood lamellae subtriangular, with short marginal setae.

Remarks:

The species has not been taken since the original lot, possibly because of closure of whaling industry (since 1962). *Cyamus bahamondei* Buzeta, 1963, from the North Atlantic region, differs from *C. (M.) catodontis* in having two pairs of ventral spines on peraeon 7, and the accessory gills (male) are equally bifurcated, with tips rounded (Leung 1967).

Cyamus (Mesocyamus) orubraedon Waller, 1989

(Fig. 11)

Material Examined:

Northwest Pacific Ocean, 44°29' N,149° 26' E; ex jaws of Baird's beaked whale *(Berardius bairdii)* - many specimens, including males and females (ov.); sent to Leo Margolis by Dr. Yuk-Maan Leung, 24 April, 1964; (PBS B6-64).

California (locality undet.), ex *Berardius bairdii* - 1 vial of specimens, identified for Dale Rice, February and again in April, 1964, CMN collections.

California & Japan (localities undetermined), ex *Berardius bairdii;* 2 vials of specimens identified for Y.M. Leung, April, 1964, CMN collections.

West coast Vancouver I., ex *Berardius bairdii*, Aug. 14, 1964 - male (8 mm), slide mount, (PBS B5-95), CMN coll's.

Diagnosis: Male (8.0 mm).

Body relatively slender, widest at peraeon segment 3; peraeon segment 2 narrow, subrectangular; segments 3 & 4 narrow, wings widely separated; peraeon segments 5 & 6 laterally reflected; peraeon segment 7 deep, subtriangular, hind margin subtruncate.

Head elongate, broadened at fused peraeon segment 1. Eyes medium, oval. Antenna 1 short, 4-segmented; segments 1 & 2 stout, 2 the shorter. Antenna 2 medium, 4-segmented.

Mouthparts: Upper lip medium broad, lower margin sharply notched, finely setulose; lobes subequal. Lower lip, outer lobes narrow, not widely separated, inner distal margin nearly straight, richly short-setose; inner lobes slightly separated apically. Mandible short, broad; incisor 5-dentate; molar flat, minutely pilose, with proximal seta; left lacinia large, 5-dentate, with single small proximal blade; right lacinia trifid, with 2 short proximal blades. Maxilla 1 large, apical margin of outer plate oblique, armed with with 7 (6) longish pectinate spine-teeth. Right palp relatively large and thick, inserted mainly distally, with strong apical setae only. Maxilla 2 medium; inner plate distinct, relatively large, with 1 apical seta, little exceeded by broad outer plate, apex convex, with stiff setae. Maxilliped palp lacking in adults; segment 2 (basis) medium, fused proximally with opposite member, with small, nearly bare lobe (2 setae), little exceeded by rounded apically setose segment 3.

Gnathopod 1 slender, 6-segmented; propod palm medium oblique, palm short. Gnathopod 2 powerful, appearing 4-segmented; propod stout, palm shallowly concave, nearly horizontal.

Peraeopods 5-7 strong; basis short; carpus deep, toothed; propod shallowly long-ovate; dactyl strong.

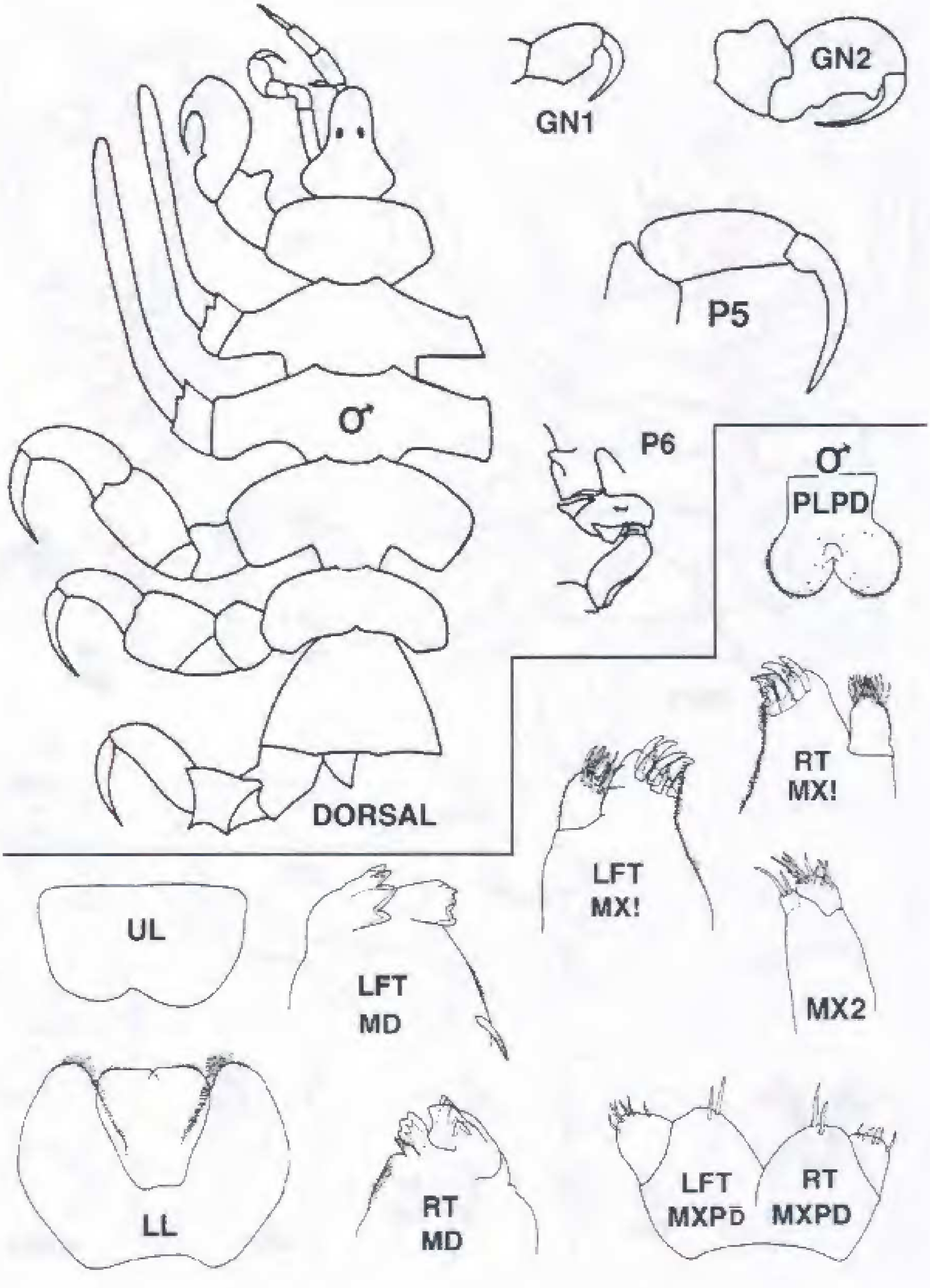

Fig. 11. ***Cyamus (Mesocyamus) orubraedon*** **Waller, 1989.** Male (8 mm), ex *Berardius bairdi*, off west coast Vancouver I., B. C. (Upper inset: after Waller 1989).

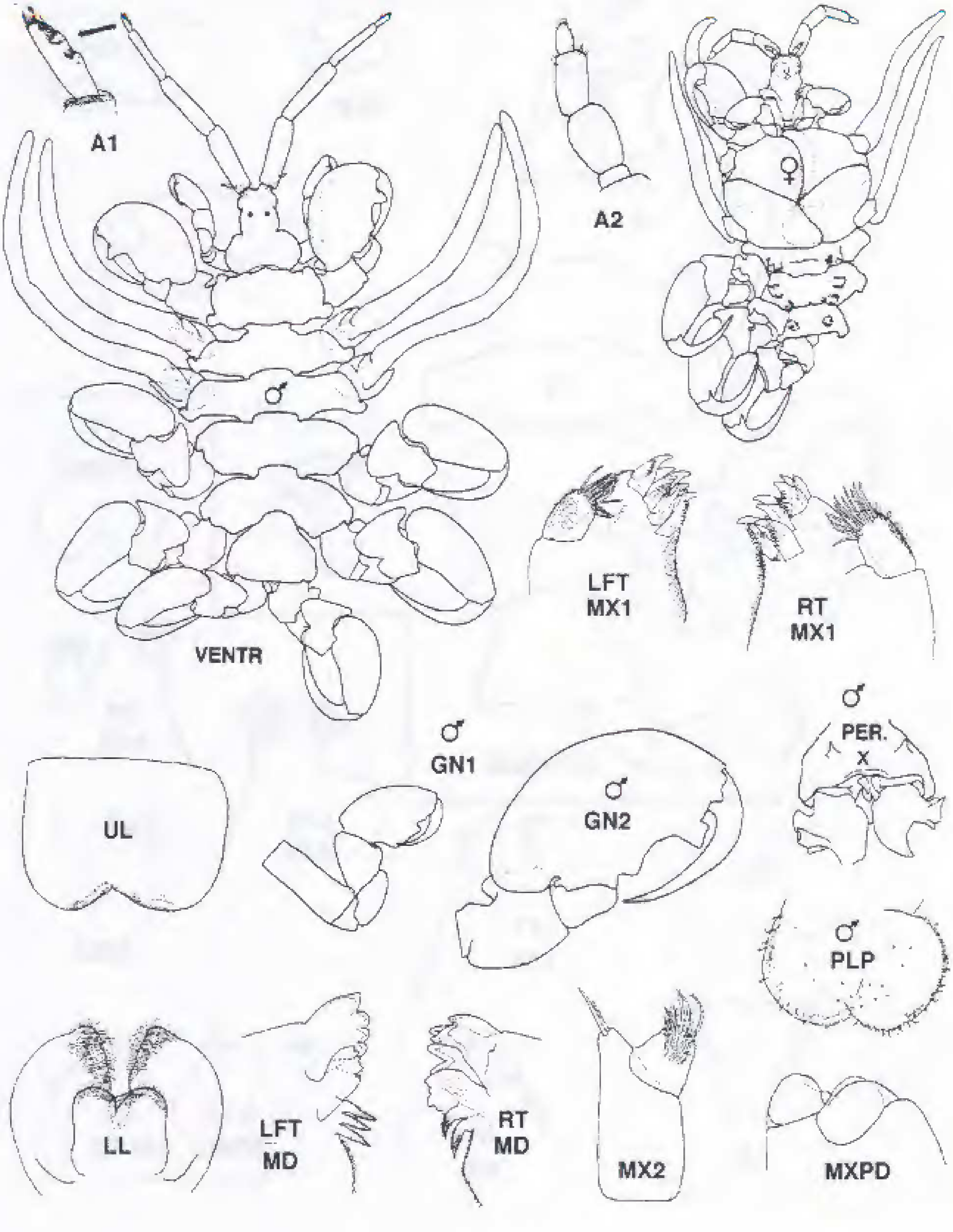

Fig. 12. ***Cyamus (Mesocyamus) mesorubraedon*** **n. sp.** Male (18 mm); female (9.5 mm) ex *Eschrichtius robustus*, Sooke, B. C.

Coxal gills single, slender. Accessory gills small, double, paired on each side.

Male pleopods medium deeply separately apically, apices rounded, strongly setulose.

Female: (to 6 mm) (not described).

Remarks:

Waller's original description and illustration of *Cyamus orubraedon* was limited and contained little information about the mouthparts. The species is known only from the beaked whale *Berardius bairdii*.

Cyamus (Mesocyamus) mesorubraedon, n. sp.

(Fig. 12)

Material Examined:

Outer coast of Vancouver Island, British Columbia, ex skin of cachelot (*Physeter macrocephalus*) (no other data?) Male (18 mm) (**Holotype**), CMNC 2000-0007; female (ov.) (6.5 mm) (**Allotype**), CMNC 2000-000; male (12 mm?), slide mount (**Paratype**), CMNC 2000-0009.

Diagnosis: Male (to 18 mm); female (to 9.5 mm).

Body large, medium, broad, widest at poeraeon segment 4; peraeon 2 subrectangular; peraeon segment 6 with two pairs of ventral adhesion spines.

Head medium. Antenna 1 strong, regular, 4-segmented; segments 1 & 2 subequal, segment 3 shorter, segment 4 apically and marginally setulose. Antenna 2 small, segments 1 & 4 short, small.

Mouthparts: Upper lip narrow, regularly incised apically, lobes unequal. Lower lip, inner lobes separated distally; outer lobes narrow, not widely spaced. Mandibular incisor 4-5-dentate; left lacinia irregularly denticulate, with 3 short blades in spine row; molar broad, flat, finely ridged, with stout proximal seta; right lacinia distally crenulate, with 2 stout proximal blades. Maxilla 1 short, broad, with 7 medium-tall pectinate spine-teeth on both sides; palp short, with narrow blade-like apical setae. Maxilla 2 small; outer plate large, rounded, apex with strong narrowly blade-like setae, distinctly exceeding small inner plate, apex with 2 setae. Maxilliped, basal segment lacking distomedial marginal setules.

Gnathopod 1 appearing 4-segmented; propod subovate, palm nearly horizontal, with strong hinge tooth and weak proximal tooth. Gnathopod 2 short, stout, 5-segmented; basis with large anterodistal flange; segment 3 distinct; segment 5 cryptic; propod short, very deep; palm short, shallowly concave, hinge and proxial teeth small, rounded; dactyl regular, not strongly curved.

Coxal gills long, slender, single, each with double accessory gills, posterior gills slightly the longer.

Peraeopods 5-7 short, compact; peraeopod 7 distinctly smallest; basis with anterior teeth or cusps; segment 3 nearly completely fused with distal protion of segment 2; segment 4 with distinct anterior margin; propod small, ovate; palm with distinct hinge tooth.

Male pleopods fused nearly totally, distal margin with small medial cleft. Penes subtriangular.

Female (ov.) (6.5 mm) (Allotype): distinctly smaller than male. Coxal gills slender, little shorter than in male. Inner margins of brood lamellae lined with fine setae.

Etymology: The species is near *C. orubraedon* and represents an intermediate conditon between primitve and advanced members of the genus *Cyamus*, hence the combining name "meso" + "rubraedon".

Remarks: *C. (Mesocyamus) mesorubraedon* co-occurs with *C. (Apocyamus)) eschrichtii* but is readily distinguished by its larger size, more elongate slender gills, and more powerful peraeopods 5-7.

Apocyamus, new subgenus

Type species: *Cyamus scammoni* Dall, 1872. Species:*Cyamus kessleri* Brandt,1872; *Cyamus eschrichtii*, new species.

Diagnosis:

Body very large and broad. Peraeon segment 2 not rectangular,broadest medially or posteriorly; peraeon ventral spines present, various; peraeon segment 7 rectangular or rounded behind.

Head short, broad, little longer than wide. Antenna 1 relatively short, segments thick.

Mouthparts modified. Upper lip, epistome weakly or not produced. Lower lip, inner lobes trending to distal fusion. Left mandible, lacinia modified, scabrous; usually 2 blades in spine row. Maxilla 1, outer plate mostly with 7 apical spine teeth on each side, inner distal margin finely setose. Maxilla 2 inner plate trending to reduction and fusion with outer plate, Maxilliped palp trending to loss in adult stage.

Gnathopod 1, palm shallow, oblique, teeth weak. Gnathopod 2 appearing 4-segmented; propod short, palm sharply concave, dactyl short. Peraeopods 5-7 not powerfully developed, propods and dactyl short.

Coxal gills stout, single or double; accessory gills paired on each side, well developed. Male pleopods with shallow distal notch.

Etymology: In balance, character states of the subgenus are considered most advanced of all subgenera within the genus, hence the name "apo" + "cyamus".

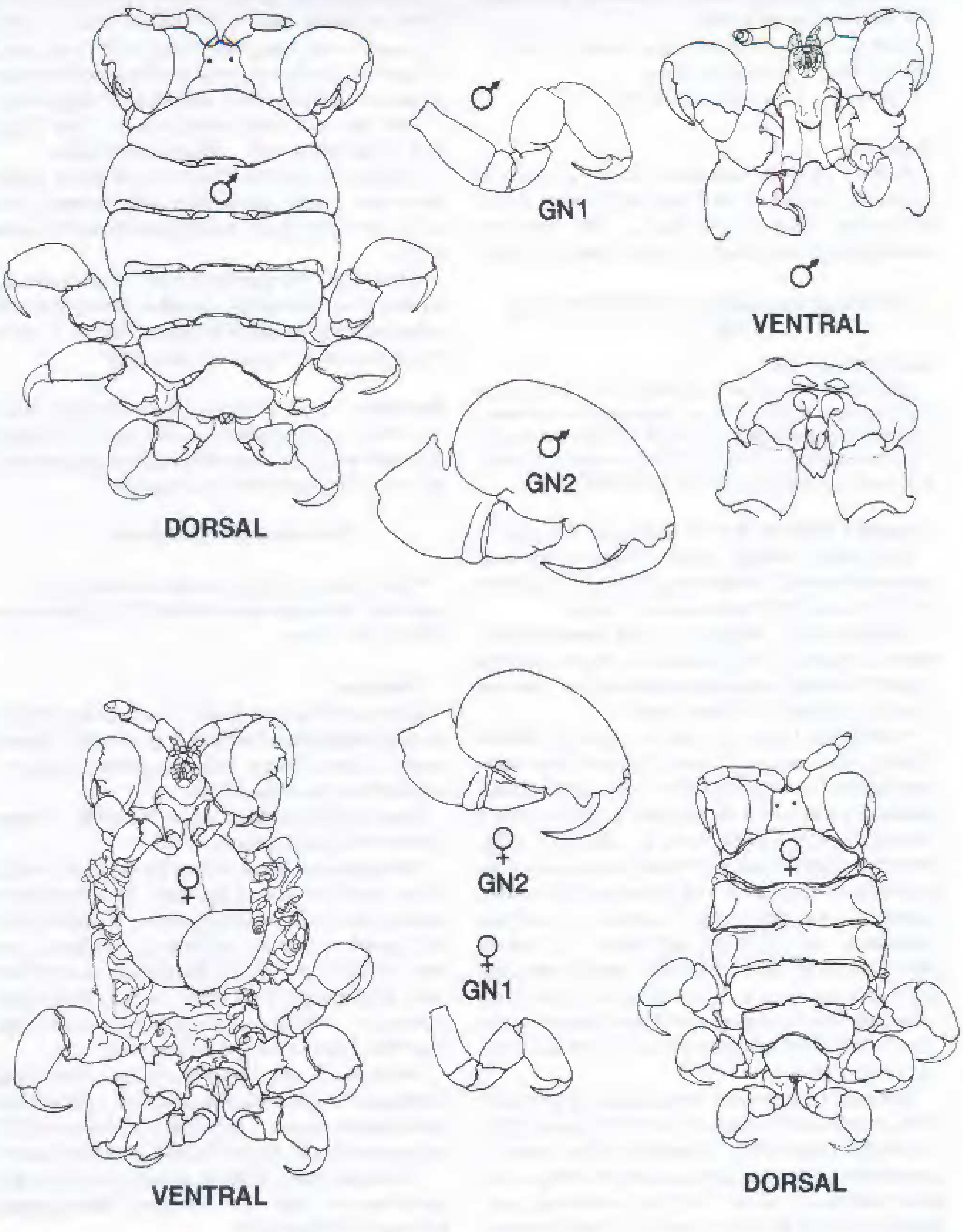

Fig. 13. ***Cyamus (Apocyamus) scammoni*** **Dall, 1872.** Male (14 mm); female (ov.) (12 mm). ex *Eschrichtius robustus*, Sooke, B. C.

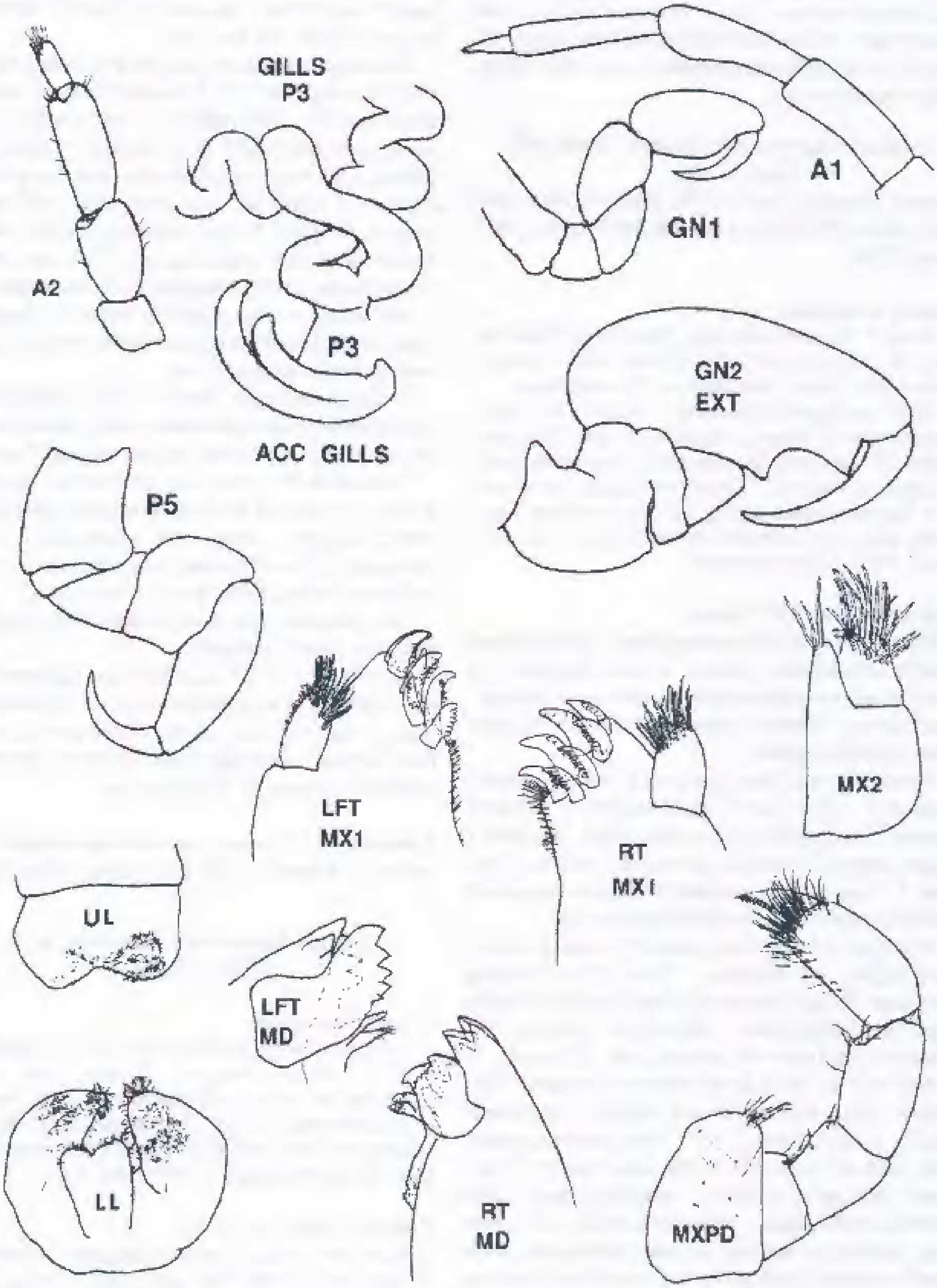

Fig. 14. *Cyamus (Apocyanus) scammoni* **Dall, 1872.** (peraeopods and mouthparts).

Remarks. Although specialized in coxal gill morphology, the type species *C. (A.). scammoni* exhibits both apomorphic and plesiomorphic character states. All species are primary ectoparasites of the Gray whale, *Eschrichtius robustus*.

Cyamus (Apoyamus) scammoni Dall, 1872
(Figs. 13, 14)

Cyamus scammoni Dall, 1872a; Andrews 1914; Margolis 1954b, 1955; Hurley & Mohr 1957; Leung 1967; Leung 1976.

Material Examined:

Sooke, B. C., ex stranded gray whale (*Eschrichtius robustus*), G. L. Fletcher coll., Oct. 29-Nov. 1/89 - ~25males, females (ov.), + imm., slide mounts, CMN collections.

California, various locations, ex ~ 20 gray whale (Dale Rice mentions Yu-Maan Leung coll.), 2 April, 1964 - large numbers of specimens (Specimens of *C. kessleri* also taken and sent to L. Margolis, 17 April, 1964), CMN collections.

St. Lawrence Island, Bering Sea, Alaska ex Gray whale - many specimens (identified for Bud Fay by L. Margolis, March, 1955), CMN collections.

Diagnosis: Male (to 27 mm).

Body very broad. Peraeon segments 3 & 4 broadest, dorsally light purple in colour. Peraeon segments 2 to 7 very broad, interspace relatively narrow, lateral margins convex. Peraeon segment 6 with pair of weak ventral adhesion spines.

Head short, very broad posteriorly at fused peraeon segment 1. Eyes small, round, weakly pigmented. Antenna 1, segments short, medium thick; segment 1 largest; segment 4 slender, apex acute, setulose. Antenna 2 4-segmented; segment 3 longest; segment 4 relatively large, apex rounded, finely setose.

Mouthparts: Upper lip shallowly notched below, lobes slightly asymmetrical. Lower lip with strong inner lobes, distally separated; outer (mandibular) lobes large, not widely spaced. Mandibular incisors 5-6 dentate; molar flat; with proximal seta; left lacinia 5-dentate,with 2+ short thick blades proximally; right lacinia with a main tooth and irregular denticules. Maxilla 1 short, broad, with 7 short pectinate apical spine-teeth on each side, inner distal margin finely setose; left palp proximal, relatively large, apex rounded, multi-setose. Maxilla 2 small; outer plate large, distinct, extending beyond inner plate, apex broadly rounded , with stiff setae; inner plate small but distinct, apex with 1-2 medium setae. Maxilliped short; palp relatively short, always present in adults; segments 4 & 5 shorter than 6; dactyl short, acute, medial margin finely pectinate; basal segment totally separated from opposite member; inner lobe distinct, margin multisetose; segment 3 with small outer lobe, margin with several short setae.

Gnathopod 1 medium strong, 6-segmented, segment 3 distinct; segments 4 & 5 subequal; propod elongate, nearly parallel-sided; palm very short, nearly vertical, lacking proximal tooth; dactyl medium, unguis fused. Gnathopod 2 stout, powerful, appearing 5-segmented; segment 3 partly fused to stout basis and shallow anterior marginal flange; segment 4 small, lacking distinct anterior margin; segment 5 narrow, cryptic; propod large, deeply elongate-ovate; palm short, unevenly concave, very shallowly oblique, hinge tooth large, acute, larger than proximal palmar tooth; dactyl medium large, gently curved.

Coxal gills elongate, double, sharply spirally coiled, arising from common basal stalk, held ventrally; accessory gills present, distinct, turgid, unequally paired.

Peraeopods 5-7 short, not very robust; segment 3 distinct; segment 4 with small anterior margin; segment 5 as deep as long, with antero-distal process overhanging base of propod; propod relatively short, subovate, lacking palm; dactyl short, curved.

Male pleopods with medium deep distal cleft. Penes short, curved medially.

Female (ov.) (to 17 mm): peraeon segments 6 & 7 each with pair of weak adhesion spines. Brood lamella large, ovate, forming circular brood pouch, margins finely setose. Coxal gills coiled as in male, held ventrolaterally; accessory gills not seen.

Remarks: *C. (Cyamus) scammoni*, the largest known species, is hosted only by *Eschrichtius robustus*.

Cyamus (Apocyamus) eschrichtii, n. sp.
(Figs. 15, 16)

Material Examined:

California, various locations, ex ~ 20 gray whales, Dale Rice & Yu-Maan Leung coll., 2 April, 1964 - several specimens, incl. males and females (ov); Ibid., male (10 mm) (**Holotype**), CMNC 2000-0004; female (8.0 mm) (**Allotype**) CMNC 2000-0005 (PBS B10-95); male (10 mm) slide mount (**Paratype**), CMNC 2000-0006.

Diagnosis: Male (to 14 mm)

Body short, broad. Peraeon segments 2-4 broadening posteriorly, interlobal space narrow; peraeon segments 5 & 6 broad, segment 7 subrectangular; ventral surfaces each with 2-3 stout, paired, medium adhesion spines.

Head short, broadened posteriorly. Antenna 1 me-

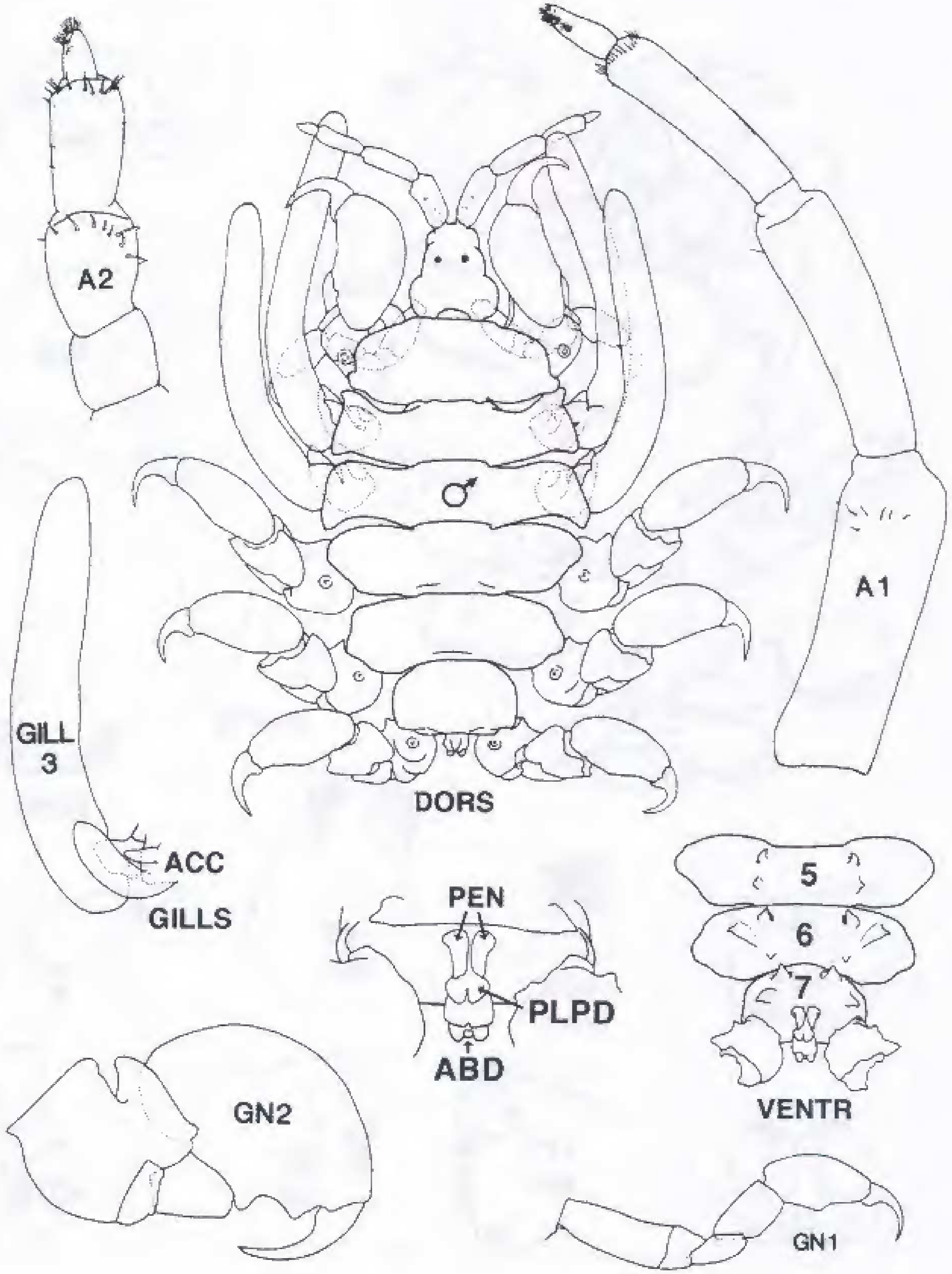

Fig. 15. ***Cyamus (Apocyamus) eschrichtii*** **n. sp.** Male (10 mm); female (ov.) (8 mm). ex *Eschrichtius robustus*, California.

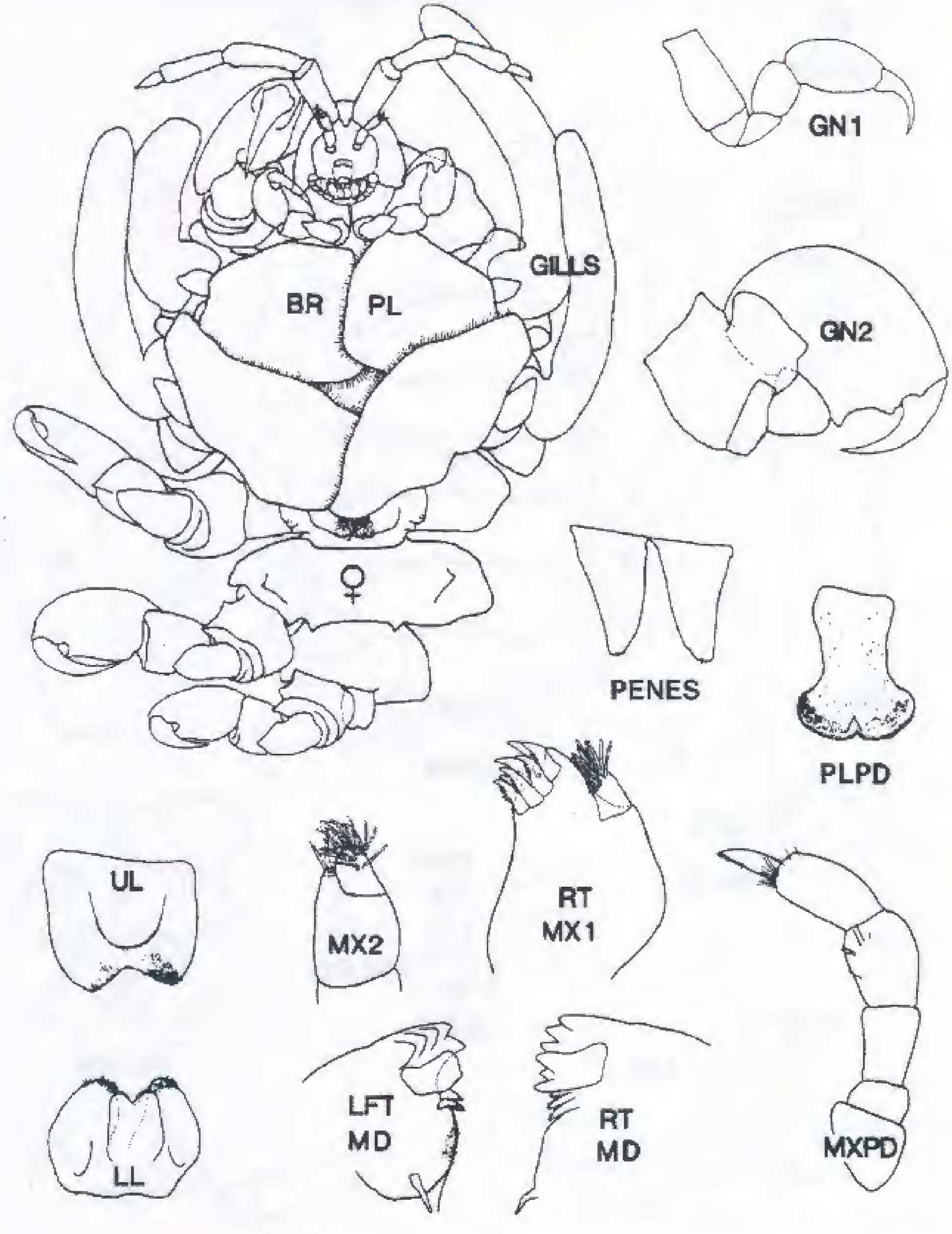

Fig. 16. ***Cyamus (Apocyamus) eschrichtii*** **n. sp.** Female (ov.) (8 mm); male (10 mm). ex *Eschrichtius robustus*, Sooke, B. C.

dium, 4-segmented; segments 1 & 2 subequal, segment 3 slightly shorter, 4 distinct, ~1/3 segment 4. Antenna 2 short, 4-segmented; segment 3 slightly longest; segment 4 with apical and subapical tufts of setules.

Mouthparts: Upper lip narrow, median notch shallow, lobes slightly asymmetrical. Lower lip, inner lobes distinct, separated distally. Mandibular incisor 5-dentate; molar weakly triturative, with proximal seta; left lacinia laminar, with 2 proximal blades; right lacinia trifid, with 3 blades in spine row. Maxilla 1, right outer plate with 7 spine-teeth, inner distal margin finely setulose. Maxilla 2, plates distinct, outer plate larger. Maxilliped palp 4-segmented, persisting in adult stage; dactyl medium long, pectinate.

Gnathopod 1 medium stout; basis slender; segment 3 large, distinct; segment 4 with short anterior margin; segment 5 long, margins subparallel; propod elongate-ovate, palm shallowly oblique and slighly concave, proximal palmar tooth low, obtuse; dactyl short, strongly curved. Gnathopod 2 short, stout, powerful, 5-segmented; basis short, thick, with strong antero-distal flange; segment 3 narrow; segment 4 distinct; propod large, deep, powerful, anterior margin arched strongly; palm short, sharply concave, nearly horizontal, hinge and proximal palmar teeth rounded apically; dactyl ordinary.

Coxal gills single, medium thick, with short basal stalk; accessory gills double, markedly unequal, posterior lobe more than twice length of anterior lobe.

Peraeopods 5-7 short, stout; peraeopod 5 slightly smallest; basis short, broad, anterior margin with proximal and distal adhesion teeth; segment 3 narrow, anteriorly fused to basis; segment 4 subcryptic, lacking anterior free margin; segment 5 medium-deep; segment 6 sub-ovate, not elongate; palm short, oblique, with weakly defined proximal tooth; dactyl short, strongly curved.

Male pleopods with shallow distal notch. Penes short, curving outwards.

Female (ov.) (8.0 mm): coxal gills shorter and thicker than in male. Posterior brood lamellae the larger, margins richly setose.

Etymology: Living on the Gray whale, *Eschrichtius robustus*.

Cyamus (Apocyamus) kessleri Brandt, 1872.

(Figs. 17, 18)

Cyamus kessleri Lütken 1873; Hurley & Mohr 1957; Leung 1967.

Material examined:

Pt. Barrow, Beaufort Sea, coast of Alaska, ex skin of gray whale *Eschrichtius robustus;* J. L. Mohr coll., 10 Aug., 1954 - male, female specimens (part of a lot identified by J. L. Mohr & D. E. Hurley; sent to Leo Margolis by J. L. Mohr, 15 July, 1957 (PBS B2-57); CMN collections.

Off Victoria, B. B., ex stranded gray whale - 1 female ov. (8 mm), slide mount, (PBS B2-57), CMN collections.

California, various locations, ex ~ 20 gray whales, Dale Rice & Yu-Maan Leung coll., 2 April, 1964 - large numbers of specimens (sent to L. Margolis, 17 April, 1964); CMN collections.

Diagnosis: Male (to 15 mm).

Body slender, widest at peraeon segment 4. Peraeon segment 2 narrow; peraeon segments 3 & 4 with blunt ventral spinous processes; peraeon segments 5 & 6 with weak ventral adhesion spines.

Antenna 1, segment 3 longest; segment 4 with apical setae only. Antenna 2, segment 2 longest.

Mouthparts: Upper lip broadly notched, lobes distinctly asymmetrical. Lower lip, outer lobes rounded; inner lobes shallow, nearly completely fused, with slight median notch. Mandibular incisor 4-5 dentate; molar appearing weakly triturative, with proximal seta; left lacinia scabrous, with 2 blades in spine row. Maxilla 1, left and right outer plates with 6 & 7 apical spine-teeth respectively; palp richly setose. Maxilla 2, inner plate partly fused with outer plate. Maxilliped palp absent in adults; segment 3 very small; basis strongly fused with opposite member.

Gnathopod 1 small; segment 3 partly fused with basis; propod deep, palm strongly concave. Gnathopod 2, segment 5 cryptic; propod large, deep, ovate; palm sharply concave, defining teeth large; dactyl short.

Coxal gills single, elongate, with weak accessory lob; accessory gills paired on each side, anterior gill longer.

Peraeopods 5-7 relatively weak; basis broad; propod short, ovate; dactyl short.

Male pleopods deeply incised apically.

Female (ov.) (to 10 mm): Body relatively broad, widest at peraeon segment 3 & 4.

Remarks:

Cyamus kessleri exhibits the broadest range of apomorphy within character states utilized here,and represents the most advanced species within the subgenus and genus *Cyamus*.

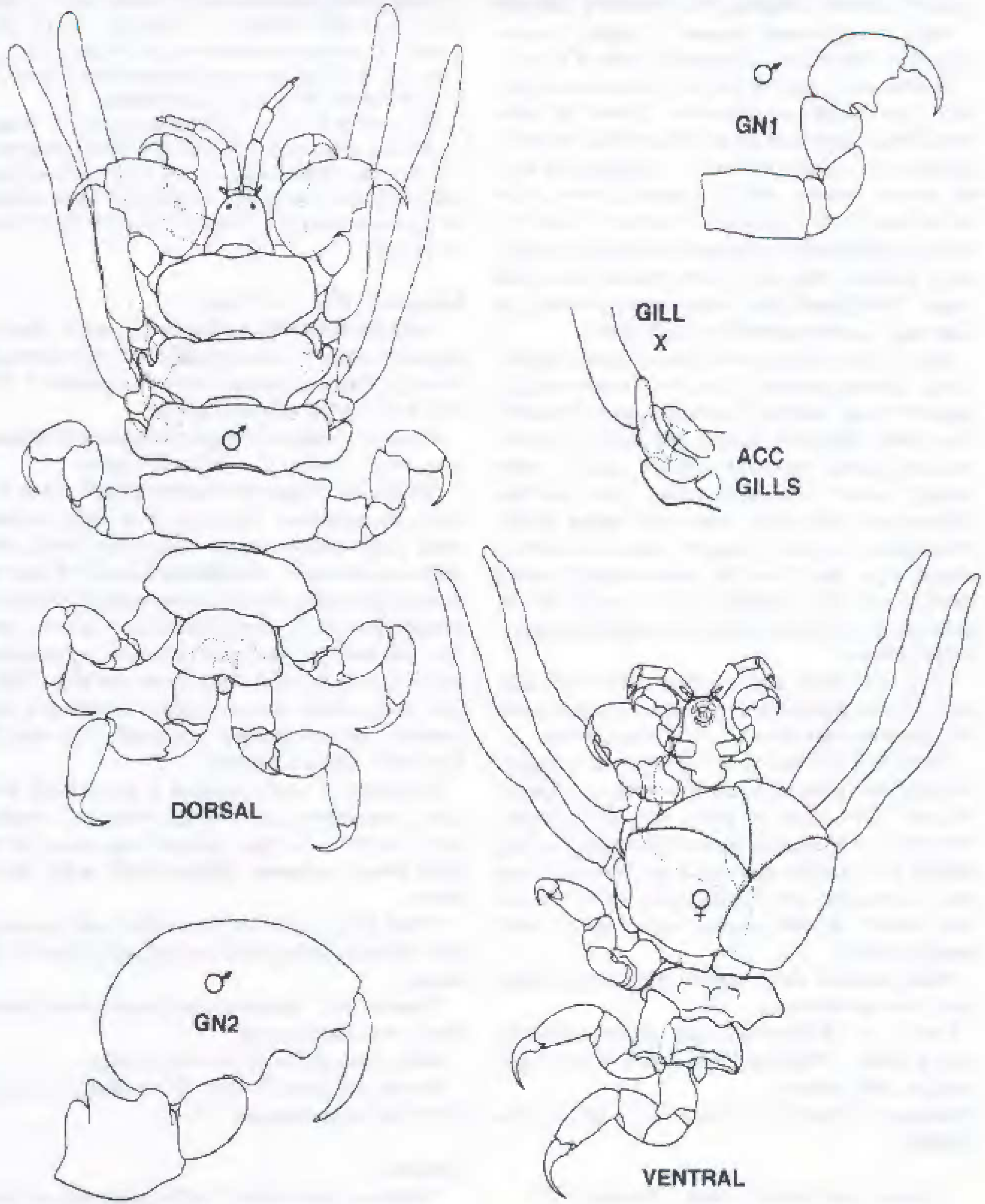

Fig. 17. ***Cyamus (Apocyamus) kessleri*** **Brandt, 1872.** Male (10.5 mm); female (8.0 mm). ex *Eschrichtius robustus*, Sooke, B. C.

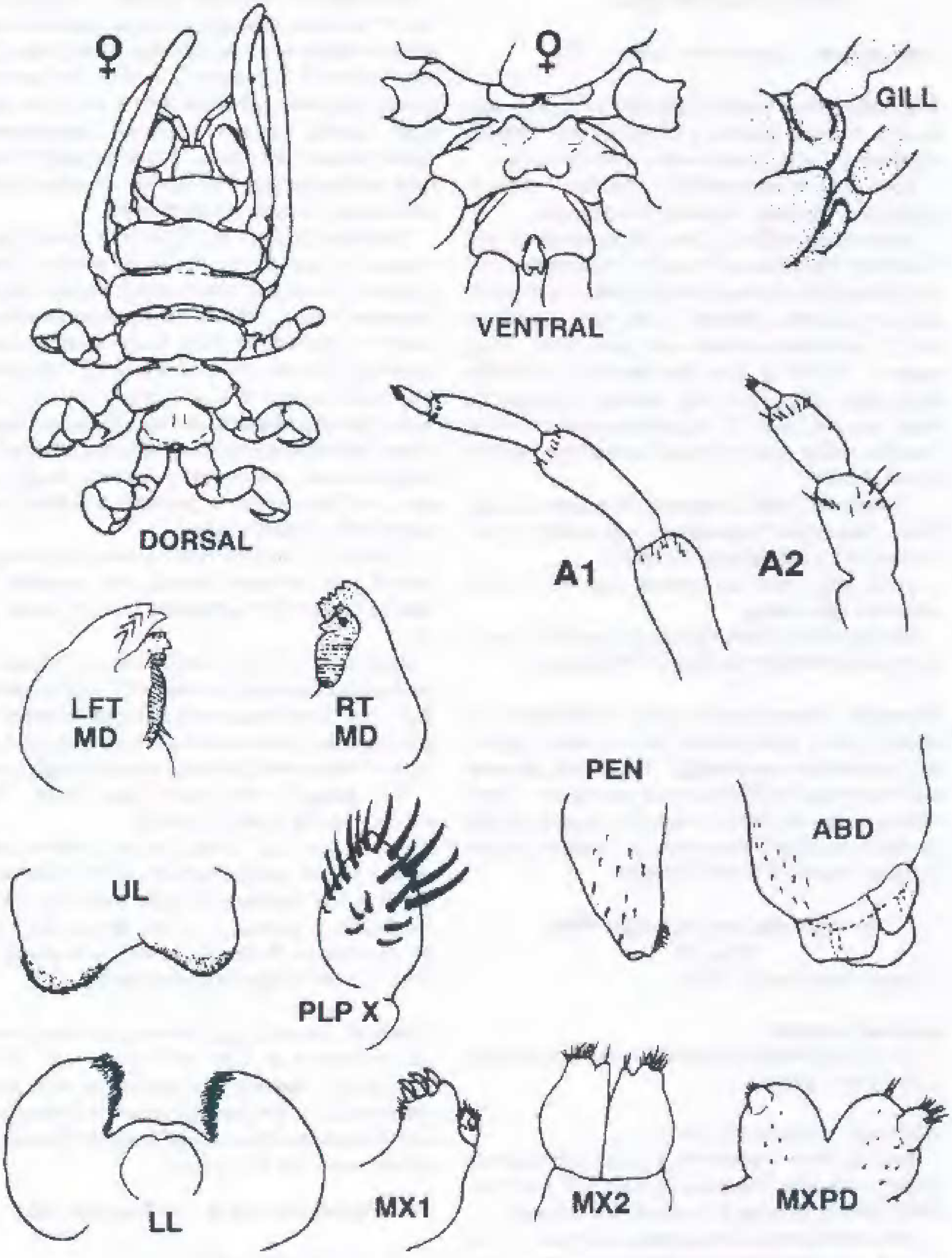

Fig. 18. *Cyamus (Apocyamus) kessleri* **Brandt, 1872.** Male (15 mm); female (10.0 mm), ex *Eschrichtius robustus*, Pt. Barrow, Alaska (after Hurley & Mohr, 1957).

Orcinocyamus, new genus

Type species: *Cyamus orcini* Leung, 1970b

Diagnosis: Body medium, broadest at peraeon segment 4. Peraeon segment 2 subrectangular. Peraeon segments 5-7 with paired ventral adhesion spines.

Head short, broad posteriorly. Antenna 1 short, 4-segmented. Antenna 2 minute, 4-segmented.

Mouthparts modified: Lower lip, inner lobes fused. Mandible: left lacinia 6-dentate(?) with proximal row of blades; right incisor and lacinia trifid(?) with proximal row of blades. Maxilla 1, outer plate apparently with 6 spine-teeth on each side; palp small, 1-segmented. Maxilla 2, inner plate lacking, fused within outer plate. Maxilliped palp lacking (all stages ?); basal segment fused 1/2 to opposite number, lacking free lobe and/or setae; segment 3 extending distinctly distad of basis.

Gnathopod 1 small, 5-segmented; unguis of dactyl fused. Gnathopod 2 appearing 4-segmented (segment 3 fused with 2 and segment 5 with 6).

Coxal gills paired on peraeon segments 3 & 4; accessory gills lacking

Peraeopods 5-7 short, appearing 5-segmented, segments not powerfully developed, dactyls short.

Remarks: *Orcinocyamus* appears intermediate between *Cyamus (Apocyamus)* and *Isocyamus*, especially in mouthpart morphology. Regrettably,the original description and figures were incomplete. Specimens were not available for this study despite the fact that the host whale *Orcinus orca* is a common species in coastal waters of British Columbia.

Orcinocyamus orcini (Leung, 1970)

(Fig. 19)

Cyamus orcini Leung, 1970b.

Material Examined:

None. Original material ex *Orcinus orca*, off Senegal, West Africa (Leung, loc. cit.).

Diagnosis: Male (to 10.5 mm).

Body medium, Lateral lobes of peraeon segments slightly separated. Peraeon segments 3 & 4 not narrowed (male); Peraeon 5-7, ventral spines weak.

Head broadened at fused peraeon segment 1. Antenna 1, segments successively shortening and narrowing distally. Antenna 2, segment 3 longest,terminal segment apically setose.

Mouthparts: as in generic diagnosis. Upper lip not described. Leung (loc. cit.) may have confused left and right mandibles in his original description Maxilla 1, outer plate with 2 groups of 3 medium long pectinate spines; palp short, proximal,with a few short apical setae. Maxilla 2 medium tall, outer plate apparently apically dentate and setose. Maxilliped palp lacking; basal segment lacking free lobe and/or setae; segment 3 extending distinctly distad of basis.

Gnathopod 1, segment 3 fused with slender basis; segment 4 small, with very small anterior margin; segment 5 as deep as long; propod slender, shallow-ovate; palm short, oblique, with stout acute proximal tooth and small distal tooth; dactyl strongly curved. Gnathopod 2 short, powerful, appearing 4-segmented (segment 3 fused with 2 and segment 5 with 6); basis with large wing-like anterior marginal flange; segment 4 short, lacking free anterior margin; propod very large, elongate-ovate; palm nearly horizontal, deeply concave, with large rounded proximal and distal tooth; dactyl short, regularly curved.

Coxal gills medium slender, somewhat sausage-shaped, each subequally paired, with common basal stalk; accessory gills apparently lacking (Leung, loc. cit).

Peraeopods 5-7 short, medium stout, 5-segmented, lacking adhesion spines; peraeopod 7 slightly smallest. Basis short, broad; segment 4 with small anterior margin; segment 5 shorter than 4 posteriorly; propod slender,narrowing distally; dactyl short, not strongly curved.

Male pleopods with narrow distal notch. Penes narrow, curving slightly outwards.

Female (ov.) (to 7.5 mm): brood lamellae subtriangular to oval, margins smooth. Coxal gills shorter than in male. Gnathopod 1, palm shallowly concave. Gnathopod 2, propod shorter and deeper, palm short, deeply concave. Peraeon 5 ventrally with pair of genital valves but lacking lateral tubercles.

Remarks. Leung (loc. cit.) without rationale, believes this species to be allied to *Cyamus ceti* and *C. monodontis*. However, in accordance with present cluster analysis, the character states of *Orcinocyamus*, especially the mouthparts, would appear closer to those of *Isocyamus* and *Neocyamus*.

Isocyamus Gervais & Van Beneden, 1859

Cyamus (part) Lütken 1870.

Isocyamus Chevreux & Fage 1925; Barnard 1932; Stephensen 1942; Leung 1967.

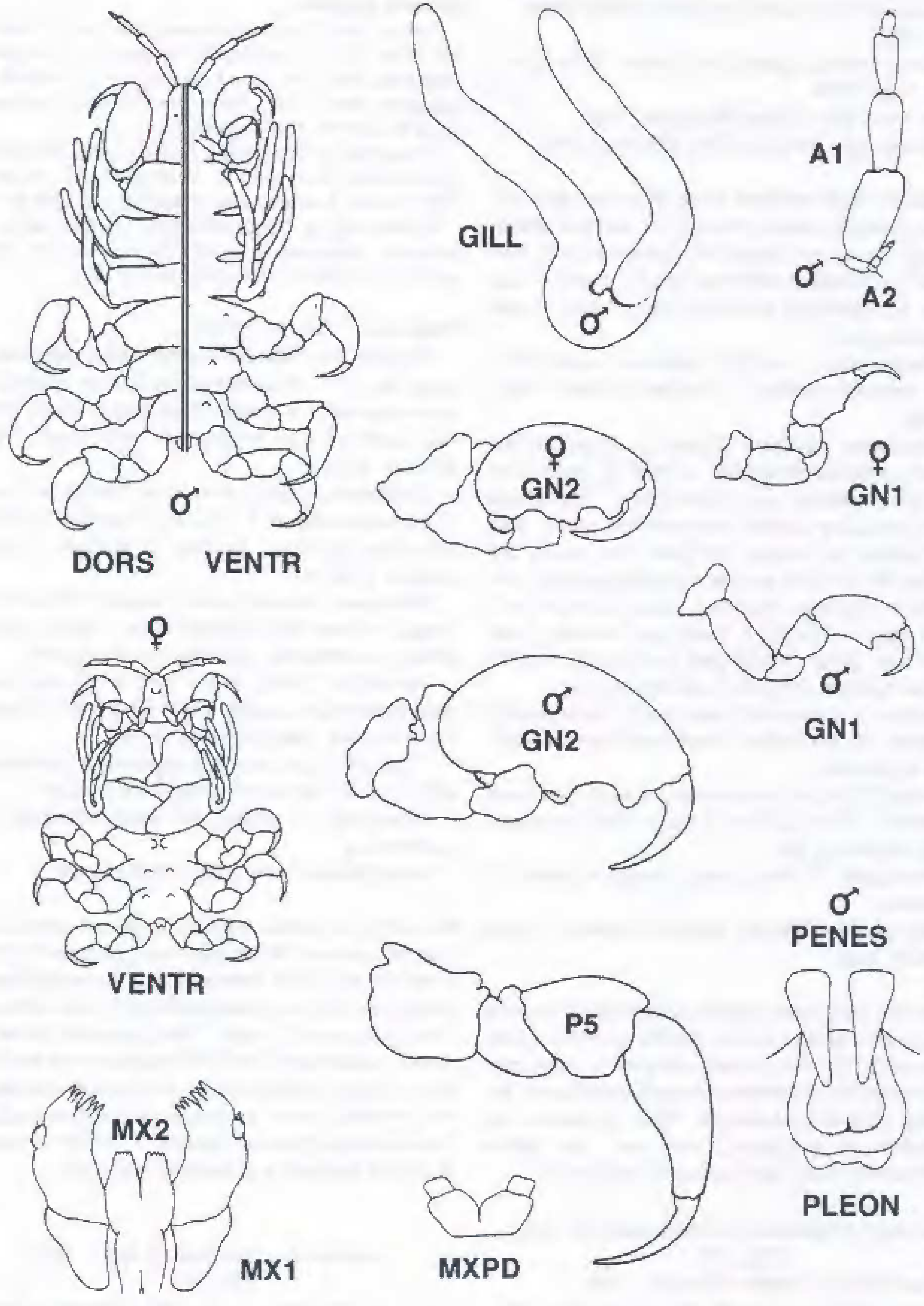

Fig. 19. ***Orcinocyamus orcini*** **(Leung, 1970b).** Male (10.5 mm); female (ov.)(7.5 mm), ex *Orcinus orca*. Atlantic Ocean, off Dakar, Senegal.

Type species: *Isocyamus delphinii* (Guérin-Méneville, 1836).

Species: *Isocyamus globicipitis* Lütken, 1873; Chevreux & Fage 1925.
Isocyamus kogiae Sedlak-Weinstein, 1992.
Isocyamus spp. Bowman 1955; Bowman 1958.

Diagnosis: Body medium broad. Peraeon segment 1 broadest, shield-shaped, and may be notched anterolaterally. Peraeon segments 3 & 4 narrowed, each with paired latero-ventral adhesion spines; peraeon segments 5-7 separated, each with pair of stout ventral adhesion spines.

Head medium. Antenna 1 medium, 4-segmented, basal segments thickened. Antenna 2 short, 3-segmented.

Mouthparts modified. Upper lip large, notched apically, lobes asymmetrical. Lower lip, outer lobes narrowly separated; inner lobes fused. Mandibular molar forming a rounded setulose knob, surface with short blades but lacking proximal seta; incisor 5-6 cuspate; left lacinia 5-dentate, right lacinia trifid?; 0-2 blades in spine row. Maxilla 1, outer plate with 6 or 7 apical spines. Maxilla 2, inner plate obsolete, fused with outer plate. Maxilliped, basis small, weakly setulose apically, segment 3 and palp lacking.

Gnathopod 1 medium, 5-segmented; dactyl distally pectinate, unguis distinct. Gnathopod 2 stout, appearing 4-segmented.

Coxal gills single, short, stout , on each of peraeon segments 3 & 4, each with single large, variously shaped accessory gill.

Peraeopods 5-7 short, stout, strongly raptorial, 5-segmented.

Male pleopods deeply separated distally. Penes relatively large.

Remarks: *Isocyamus* appears intermediate between the primitive genus *Cyamus* and the advanced genus *Syncyamus*. Species currently assigned to *Isocyamus* differ markedly in character states of mouthparts, accessory gills, and peraeopods. These differences are suggestive of polyphyly, and need for further classificatory study (see discussion and Fig. 31).

Isocyamus delphinii (Guérin-Méneville, 1836)
(Fig. 20)

Cyamus delphinii Guérin-Méneville, 1836.
Isoyamus delphinii Barnard 1932; Stephensen 1942; Bowman 1958; Stock 1973; Leung 1967; Balbuena & Ragan 1991; Wardle et al. 2000.

Material Examined:

Vargas Island, Clayoquot Sound, west coast of Vancouver Island, B.C.; on trailing edge of dorsal fin of stranded false killer whale *Pseudorca crassidens*; R. Baird & K. Langellier colls., 1 Oct. ,1989 - 1 specimen (as *Isocyamus* sp). PBS B14-95, CMN collections.

Trinity Bay, Newfoundland; ex skin wounds, pilot whale (*Globicephala melaena*); D. E. Sergeant coll., October, 1952 - mature & immature males and females, PBS B6-55.

Guadalcanal, ex *Delphinus delphis* (no other data) - 2 specimens (identified for Torben Wolff, February, 1964; specimens transferred to Leung, May 18, 1971).

Diagnosis: Male (to 9 mm?).

Medium-sized cyamids, ectoparasitic on medium to large dolphins. Peraeon segment 2 large, broad; peraeon segments 3 & 4 with strong ventro-lateral adhesion spines; peraeon segments 5-7 with stout ventral adhesion spines.

Head small, slightly broadened basally at fusion with peraeon segment 1. Antenna 1, segment 1 largest, broadening distally. Antenna 2, segment 2 large: segment 3 minute.

Mouthparts: Lower lip,with fused inner lobes, inner margin of outer lobes strongly pilose. Other mouthparts as described by Stock (loc. cit. & Fig. 20).

Gnathopod 1, dactyl with 15-20 strong inner marginal pectinations, unguis small. Gnathopod 2, palm short, concave; dactyl medium strong.

Coxal gills short, stout, sausage-shaped; accessory gills large, spade-shaped, single on each side.

Peraeopods 5-7: Peraeopod 7 smallest; dactyls medium strong.

Male pleopods with shallow distal notch.

Remarks: *Isocyamus delphinii* has been recorded from several species of Dephinidae and questionably from some members of the Phoecenidae. The probability of occurrence of this cyamid species on several different host whale species is moot. This cyamid would not be entirely unexpected from Dall's porpoise and the Harbour porpoise, although no cyamid material from those two potential host whales has yet come to hand in Canad-ian Pacific coastal waters. Further material should be obtained and carefully examined.

Isocyamus globicipitis (Lütken, 1873)
(Fig. 21)

Cyamus globicipitis Lütken, 1873; Chevreux & Fage 1925.
Isocyamus globicipitis Hiro 1938.

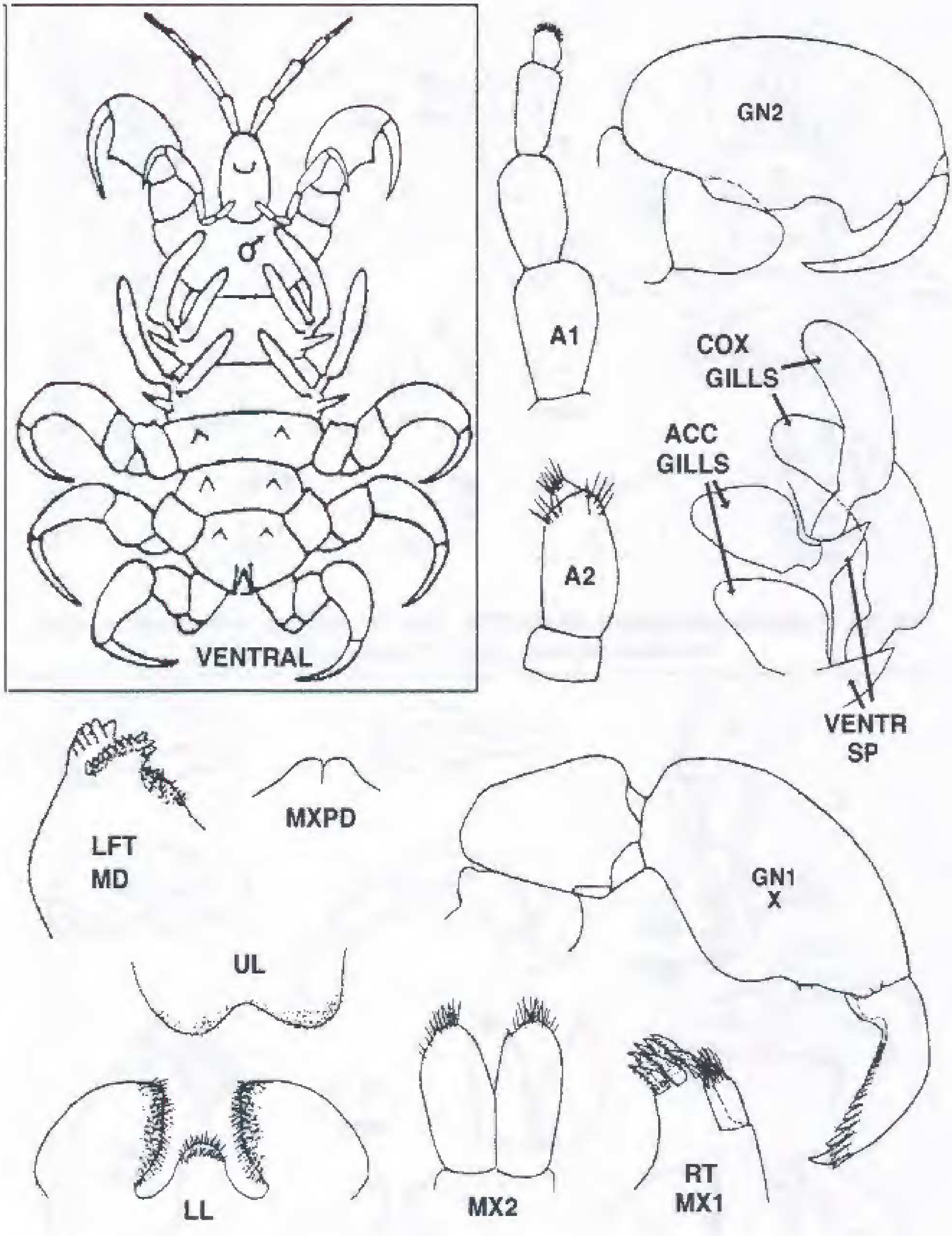

Fig. 20. ***Isocyamus delphinii*** **Guérin-Méneville, 1836.** Male (9 mm?). ex *Delphinus delphus*, North Sea region [after Stock 1973; inset: after Leung 1967).

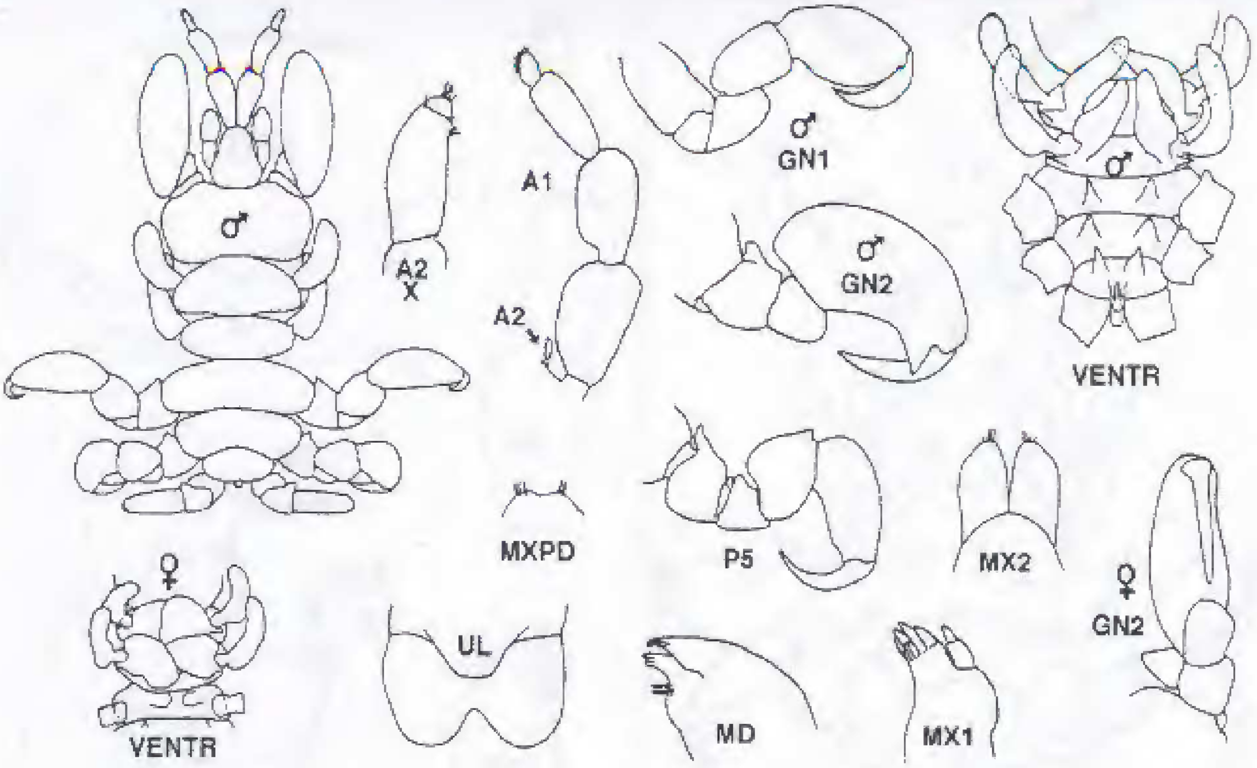

Fig. 21. ***Isocyamus globicipitis*** **Lutken, 1873.** Male (9.0 mm). ex *Globicephala melaena*, Mediterranean coast. [after Chevreux & Fage (1925)].

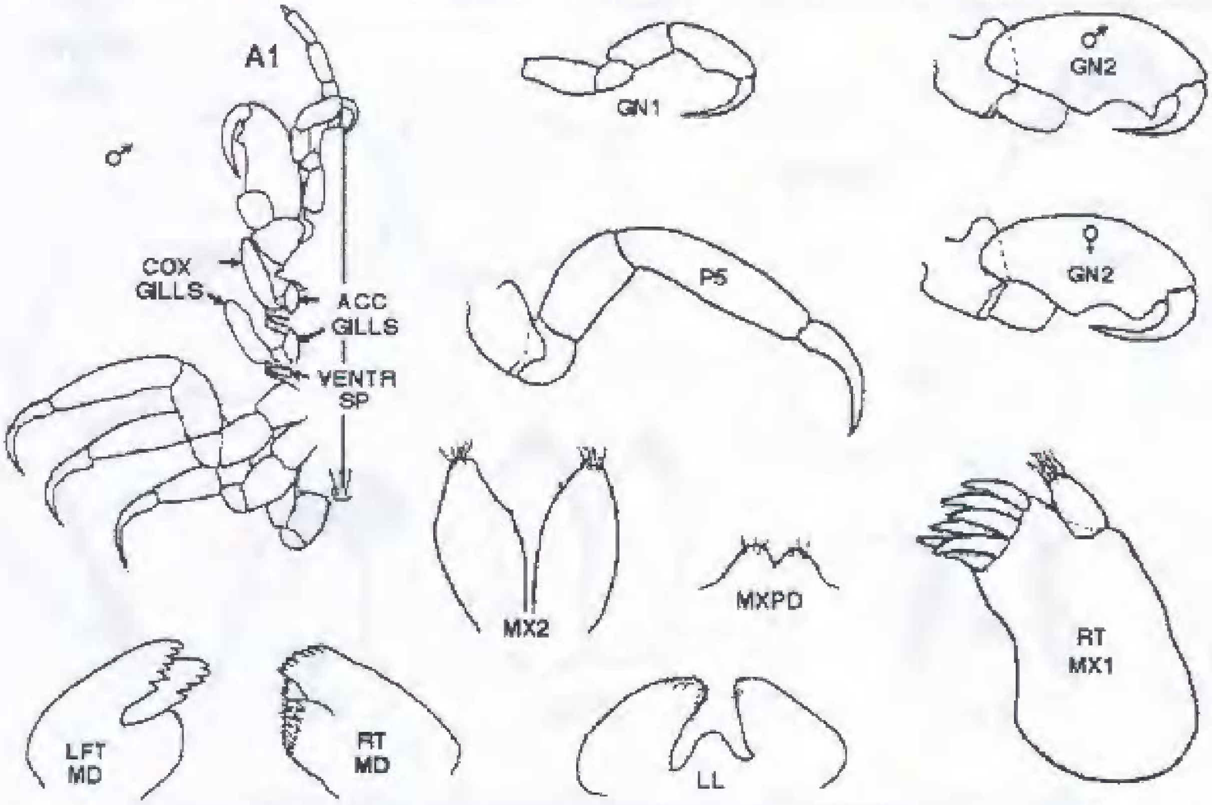

Fig. 22. ***(?)Isocyamus kogiae*** **Sedlak-Weinstein, 1992.** Male (to 5.5 mm); female (3.8 mm?). ex *Kogia breviceps* , South Australia. .

Material Examined:
None from the Pacific coast of North America.

Diagnosis: Male (to 9.0 mm); female (ov.) (to 6.5 mm) Peraeon segment 1 large, deep, slightly broader than peraeon 3 & 4; peraeon segment 5-7 with prominent ventral spines. Head somewhat elongate, lateral margins of fused peraeon 1 not bulging laterally. Maxilla 2, outer plate with 7 apical spine-teeth; palp apparently 2-segmented. Gnathopod 1, dactyl with fused unguis (not clearly demarcated).

Remarks:
The description by Chevreux & Fage (loc. cit.), of *Isocyamus globicipitis* from the bottlenose dolphin in the Mediterranean region differs from the diagnosis of Stock (1973) based on material taken from *Delphinus* from the North Sea region. Most notable is the 7 apical spine teeth and 2-jointed palp of the maxilla 1 described by Chevreux & Fage (loc. cit.).

Isocyamus kogiae Sedlak-Weinstein, 1992.

(Fig. 22)

Remarks: Sedlak-Weinstein (loc. cit.) has recently described this species from the pygmy sperm whale in Australian waters. *Kogia breviceps* is a relatively rare visitor to the Northeastern Pacific region (Orr 1972; Spalding 1998) but cyamid ectoparasites, probably of this type, might be expected to occur on them.

Sedlak-Weinstein's description of *Isocyamus kogiae* conforms somewhat with diagnostic features of the genus (e.g., in having medum long head, and comb spines on the dactyl of gnathopod 1 (but lacking unguis?). However, this species differs from *I. delphinii* in several character states including: small size; lack of right mandibular lacinia; shallower and less broadened peraeon segment 2, with anterolateral "epaulettes" (as in *Syncyamus*); peraeon 5-7 lacking ventral spines (both sexes); and segments of peraeopods 5-7 very slender and elongate. Some of these may prove to be of generic or subgeneric value (see Fig. 31).

Neocyamus Margolis, 1955

Type species: *Cyamus physeteris* Pouchet, 1888.
Neocyamus physeteris Margolis 1959; Buzeta 1963; Leung 1967.

Diagnosis: Body slender, widest at peraeon segments 5 & 6. Peraeon 2-4, lateral lobes small. Peraeon 5-7 each ventrally with pair of stout adhesion spines.

Head elongate, widest posteriorly. Antenna 1 short, 4-segmented. Antenna 2 very small, 2-segmented.

Mouthparts modified: Lower lip, inner lobes fused to medium tall plate. Mandible: incisors 5-toothed; molar eobsolete; left lacinia 5-dentate, right lacinia tridentate, 1-3 blades in each spine row. Maxilla 1, outer plate with 7 pectinate spine-teeth. Maxilla 2 tall, inner plate fused with outer plate. Maxilliped palp lacking in adults, 4-segmented in juveniles; basis small, fused 1/2 with opposite member; segment 3 extending beyond basis in adults.

Gnathopod 1 6-segmented; segment 3 distinct; dactyl pectinate, unguis distinct. Gnathopod 2 appearing 4-segmented; segment 2 (basis) elongate; segment 4 lacking anterior margin, convex behind; propod elongate, broadening distally, palm sharply concave, with strong hinge tooth; dactyl strongly curved.

Coxal gills single, multi-filamentous (fasciculate); accessory gills lacking in males.

Peraeopods 5-segmented; basis with small adhesion spine; segment 4 elongate, anterior margin with distal tooth; segment 5 with strong posterior adhesion tooth; propod slender, elongate; dactyl strong.

Male penes strong, curving medially.

Female (ov.) (to 6.0 mm): posterior brood lamellae large, margins unlined.

Remarks: *Neocyamus* is slightly more advanced than *Orcinocyamus* in the condition of antenna 2, and in some mouthpart morphology, but retains several plesiomorphic features of *Cyamus*.

Neocyamus physeteris (Pouchet, 1888)

(Figs. 23, 24)

Cyamus physeteris Pouchet, 1888.
Cyamus fascicularis Verrill, 1902; Kunkel 1910.
Paracyamus physeteris Stephensen 1942.
Neocyamus physeteris Margolis 1955; Leung 1967.

Material Examined:

Off west coast, Vancouver Island, B.C., ex sperm whale (*Physeter macrocephalus*), D. W. Rice coll., 7 April, 1956 - 2 males, 1 female, slide mounts (PBS B1-59), CMN coll'ns.

North Sea (?), ex skin sperm whale (*Physeter catodon*), A. Pouchet coll., 18 Nov., 1871 - 1 mature female, 1 mutilated male, several juveniles (obtained from Dr. Torben Wolff, Copenhagen Museum, 4 April, 1954 (PBS B25-54).

Off San Francisco, California, ex 2 sperm whales, Rice, 14 Oct., 1965 - 6 specimens (sent to L. Margolis, PBS), CMN collections.

Kurile Islands, ex *Phocoenoides truei* - 1 immature specimen (identified as *Neocyamus ?physeteris*, for Y.M. Leung, August, 1964. (See Leung 1967, p. 280).

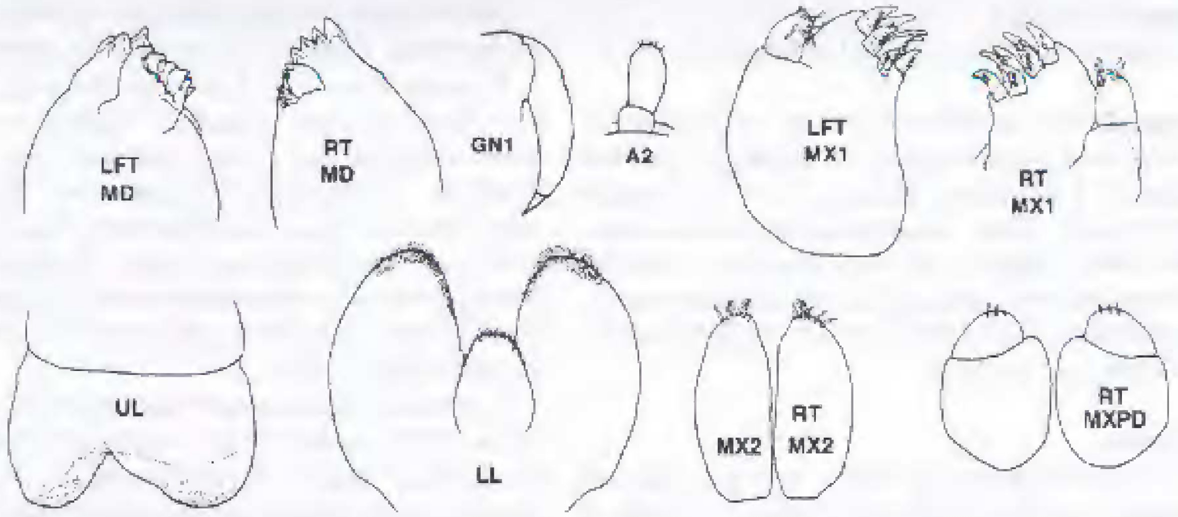

Fig. 23. ***Neocyamus physeteris*** **(Pouchet, 1888).** (mouthparts and appendages)

Diagnosis: Male (7.8 mm)

Body slender, widest at peraeon segments 5 & 6. Peraeon 2-4, lateral lobes small, widely separated; peraeon 7 subtriangular, posteriorly truncate.

Head elongate, fused segment 1 "bulging" on each side; eyes relatively large, multifacetted. Antenna 1 not longer than head length; segments 1-3 slender, subequal, segment 4 distinct. Antenna 2, segment 2 longest, rounded, apex finely setulose.

Mouthparts: Upper lip narrow, deep, apically deeply incided, lobes asymmetrical. Lower lip, outer lobes medium broad, not widely separated apically. Mandibular incisor 5-6 dentate; left lacinia broad, 5-dentate, with 1 short proximal blade; right lacinia short, thick, apex with 3 small teeth, three distinct proximal blades in spine row. Maxilla 1 short, thick, apices strongly oblique; palp short, thick, with short apical setae, medially sited. Maxilla 2 tall, inner plate not discernible. Maxilliped palp, segment 3 subtriangular, extending beyond basis, apex setulose.

Gnathopod 1, segment 3 distinct, segment 4 with small free anterior margin; segment 5 subtriangular, with small posterior lobe; propod shallow-ovate, palm oblique, concave, with weak hinge-tooth and strong rounded posterior palmar tooth; dactyl strongly curved distally finely pectinate, unguis distinct. Gnathopod 2 slender; segment 3 fused with segment 2 and segment 5 with 6; segment 4 with small anterior free margin; propod elongate, palm sharply concave, with strong acute hinge and posterior palmar teeth; dactyl large, very strongly curved.

Peraeopods 5-7 slender; basis stout, slightly longer than wide, hind margin distally with small adhesion spine; segment 3 nearly totally fused with 2, segment 4 elongate, with long free margins of which anterior margin is variously tooth-like distally; segment 5 short, subtriangular, poster lobe extended as strong curved adhesion tooth; propod slender, parallel-sided; dactyl very large, strongly hook-shaped.

Pleopods (male) rounded, distal notch indistinct. Penes large, slightly curved inwards.

Remarks: *Neocyamus* seems closest to *Isocyamus* but differs in its 2-segmented antenna 2, fasciculate coxal gills, but lack of accessory gills and lack of maxillipedal palp in adults. Several other differences in form of gnathopods, mouth parts, and form of peraeopods are also noteworthy.

Platycyamus Lütken, 1870

Type species: *Platycyamus thompsoni* (Gosse, 1855) Lütken 1870.
Species: *Platycyamus flaviscutatus* Waller, 1989.

Diagnosis:

Body slender, widest at peraeon segment 5; segments 3 & 4 narrowed, each with single ventro-lateral adhesion spines; peraeon segments 1 & 2 distinct; segments 6 & 7 not fused; segments 5 -7 each with single pair of ventral adhesion spines.

Head short, broad. Antenna 1 short, 4-segmented. Antenna 2 small, 4-segmented, sexually dimorphic.

Mouthparts modified. Upper lip apically rounded. Lower lip, outer lobes broadly separated; inner lobes fused. Mandibular molar a rounded mound, lacking proximal seta; left lacinia 5-dentate, right lacinia trifid,

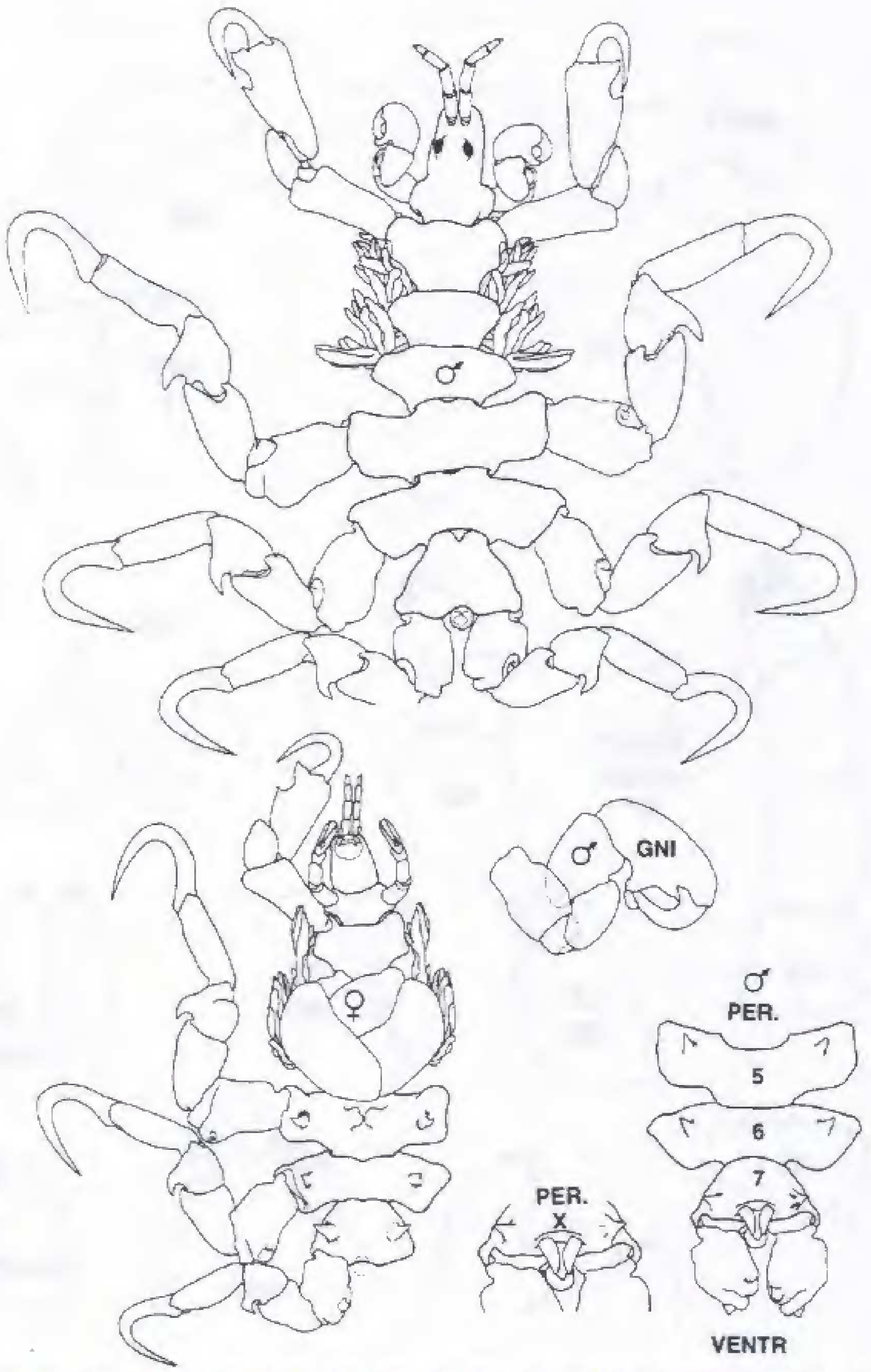

Fig. 24. ***Neocyamus physeteris*** **(Pouchet, 1888).** Male (7.8 mm); female (6.0mm?) ex *Physeter macrocephalus*, off west coast of British Columbia.

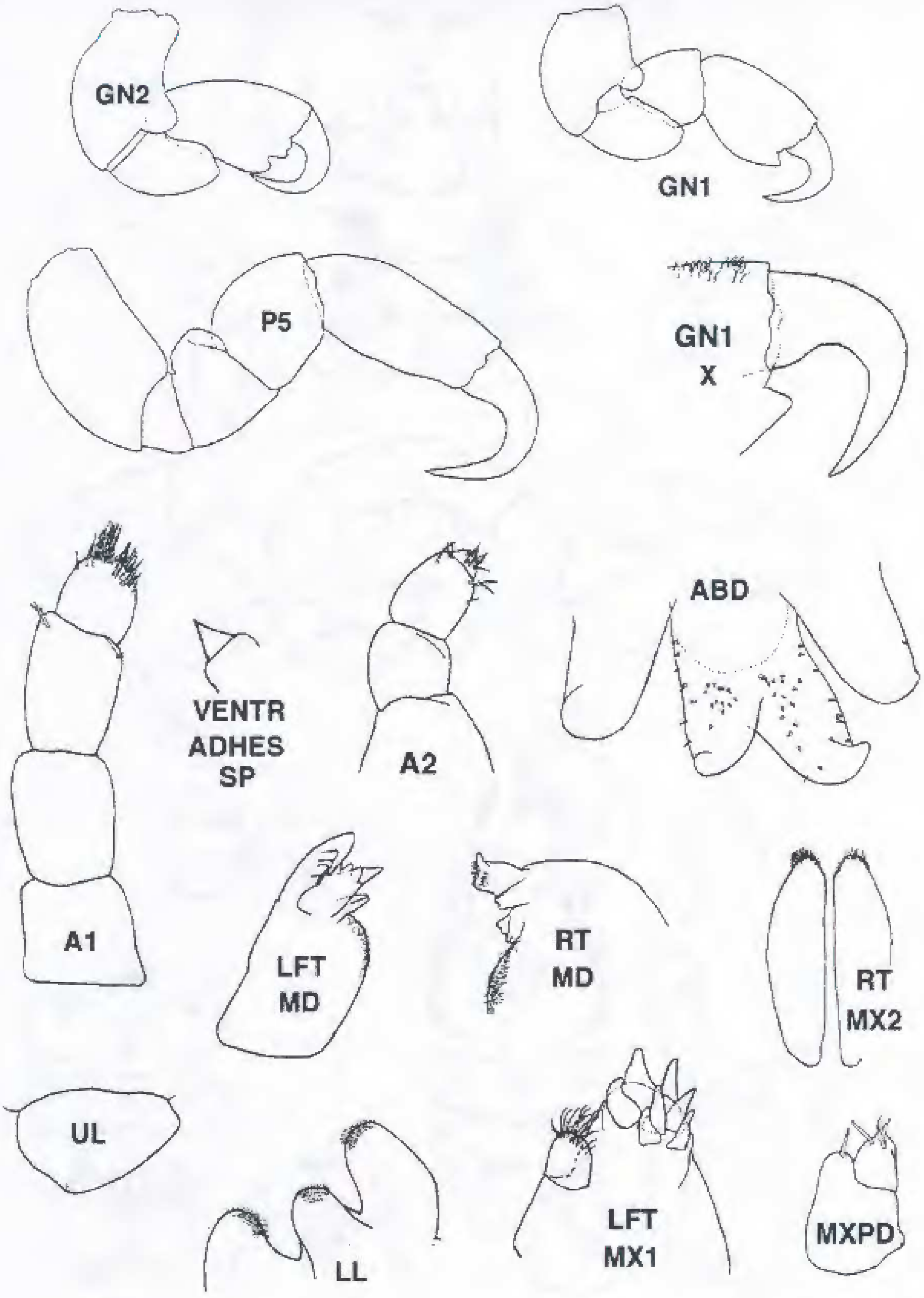

Fig. 25. ***Platycyamus flaviscutatus*** **Waller, 1989.** Male (9.0 mm, ex *Berardius bairdi* (giant bottlenose whale), off B. C. coast.

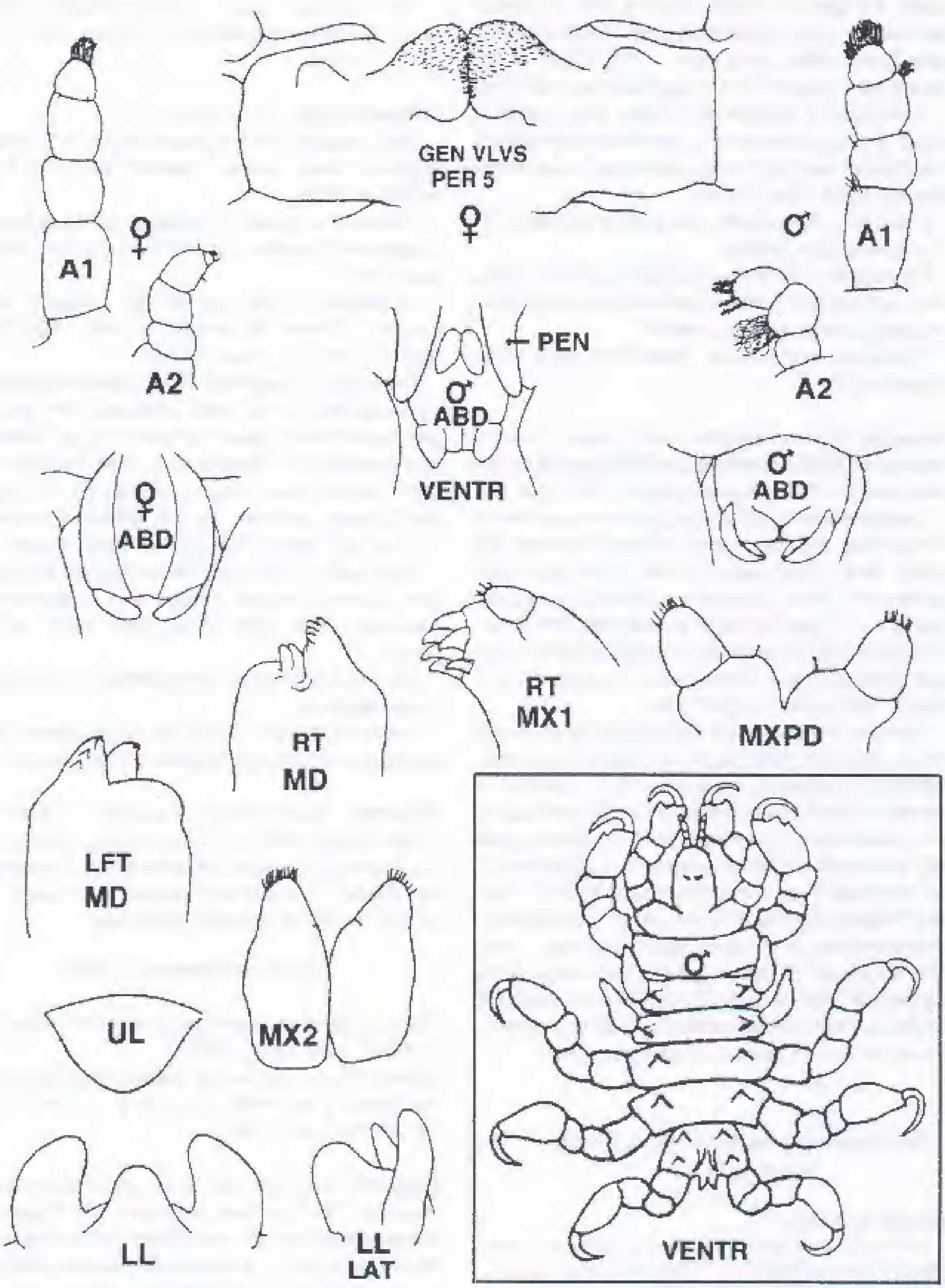

Fig. 26. ***Platycyamus thompsoni*** **(Gosse, 1855)** (mouthparts and abdomen), ex *Hyperoodon ampullatus* (bottle-nosed whale), North Sea (after Wolff 1958; Inset: after Leung 1967).

incisor 5-cuspate; 1-3 blades on each side. Maxilla 1, outer plate with 6-7 apical spine-teeth. Maxilla 2, inner plate fused within outer plate. Maxilliped small, lacking palp; segment 3 exceeding basis, apex setulose.

Gnathopod 1 6-segmented; palm short, vertical; dactyl strongly curved, unguis not clearly demarcated. Gnathopod 2 medium strong, appearing 5-segmented; propodal palm short, vertical.

Coxal gills short, double, on peraeon segments 3 & 4; accessory gills lacking.

Peraeopods 5-7 stout, 6-segmented, segments long; basis and segment 3 with spinose anteroventral process; dactyls large, strongly curved.

Male penes large, curved. Pleopods markedly separated distally.

Remarks: The two described species differ in several respects especially mouthparts and peraeopods, but are here considered congeneric (compare Figs. 25 & 26).

Consideration has also been given to recognition of *Platycyamus* and *Syncyamus* as distinctive at the subfamily level. Both genera differ from most other members of family Cyamidae in having: (1) peraeon segment 1 not fused to the head and/or fused with peraeon segment 2; (2) peraeopod 1 large, attached to peraeon segment 1 or to fused peraeon segments 1 & 2; propod with vertical toothed palm.

However, recognition of a subfamily taxon depends mainly upon interpretation of the morphological relationships of peraeon segment 1. If it represents a primary separation of the peraeon from the head region, as in gammaridean amphipods, then the character state may be considered fundamentally plesiomorphic. On the other hand a secondary detachment from the "classical" caprellidean head region might be considered a synapomorphic or autapomorphic condition. However, cognizant of current limited knowledge of the ectoparasiic fauna of several potential host ziphiid and delphniid whale species, subfamily level characterization at this time is here considered premature.

Platycyamus flaviscutatus Waller, 1989
(Figs. 25)

Material examined:

Off west coast Vancouver I., B. C., ex. Baird's beaked whale *(Berardius bairdi)*, G. C. Pike coll., 28 July, 1953 - 1 male (9 mm), slide mount, 1 female, (sent to J. Mohr (USC), identified by Mohr as *Platycyamus thompsoni*; sent from Dr. Yuk-Maan Leung, 23 Aug. 1964 (PBS B8-64), CMN colls.

Off California, coast , ex *Berardius bairdii* (no other data) - 1 specimen (mentioned by D. Rice), 22 Oct., 1965, CMN collections.

Diagnosis: Male (to 9.0 mm):

Body slender, widest at peraeon segment 5. Peraeon segment 1 small; peraeon 7 narrow; peraeon 5-7, ventral spines strong.

Antenna 1, segments 1-3 subequal in length. Antenna 2, segment 1 broadest; segment 2 with fine curly medial setae (male).

Mouthparts: Upper lip apically rounded, nearly smooth. Lower lip, margins smooth. Maxilliped, segment 3 weakly setose apically.

Gnathopod 1, basis with antero-distal rounded process; segment 5 with short posterior lobe; palm of propod very short, sharply concave; unguis faintly (or not) demarcated. Gnathopod 2, basis similarly with antero-distal process; segment 4 large; palm of propod small, sharply concave, vertical, palmar teeth large.

Coxal gills short, thick, posterior pair largest.

Peraeopods 5-7 slender; basis elongate, lacking adhesion spines; segment 4 larger than 5; propod elongate-ovate, with slight distal palm; dactyl strongly curved.

Male pleopods deeply incised apically. Penes large, diverging apically.

Female (6.0 mm): Coxal gills, apices acute. Brood lamellae, inner margins incised, sparsely setose.

Remarks: *Platycyamus flaviscutatus* is similar to the North Atlantic species *Platycyamus thompsoni* (Fig. 26), that occurs on the bottlenose whale, *Hyperoodon ampullatus*. Differences however, may justify subgeneric or possibly generic distinction.

Syncyamus Bowman, 1955

Type species: *Syncyamus pseudorcae* Bowman, 1955; Bowman 1958; Leung 1967.

Species: *Syncyamus aequus* Lincoln & Hurley, 1981; Mariniello et al. 1994; *Syncyamus chelipes* (Costa, 1853)?; Bowman 1958.

Diagnosis: Body short, small, broad, widest at peraeon segments 5 & 6; peraeon segments 1 & 2 appearing fused, demarcated by anterolateral marginal notch; peraeon segments 3 & 4 narrowed in male, each with paired ventral adhesion spines; peraeon segment 6 & 7 dorsally fused; peraeon segments 5-7 each with paired ventral adhesion spines.

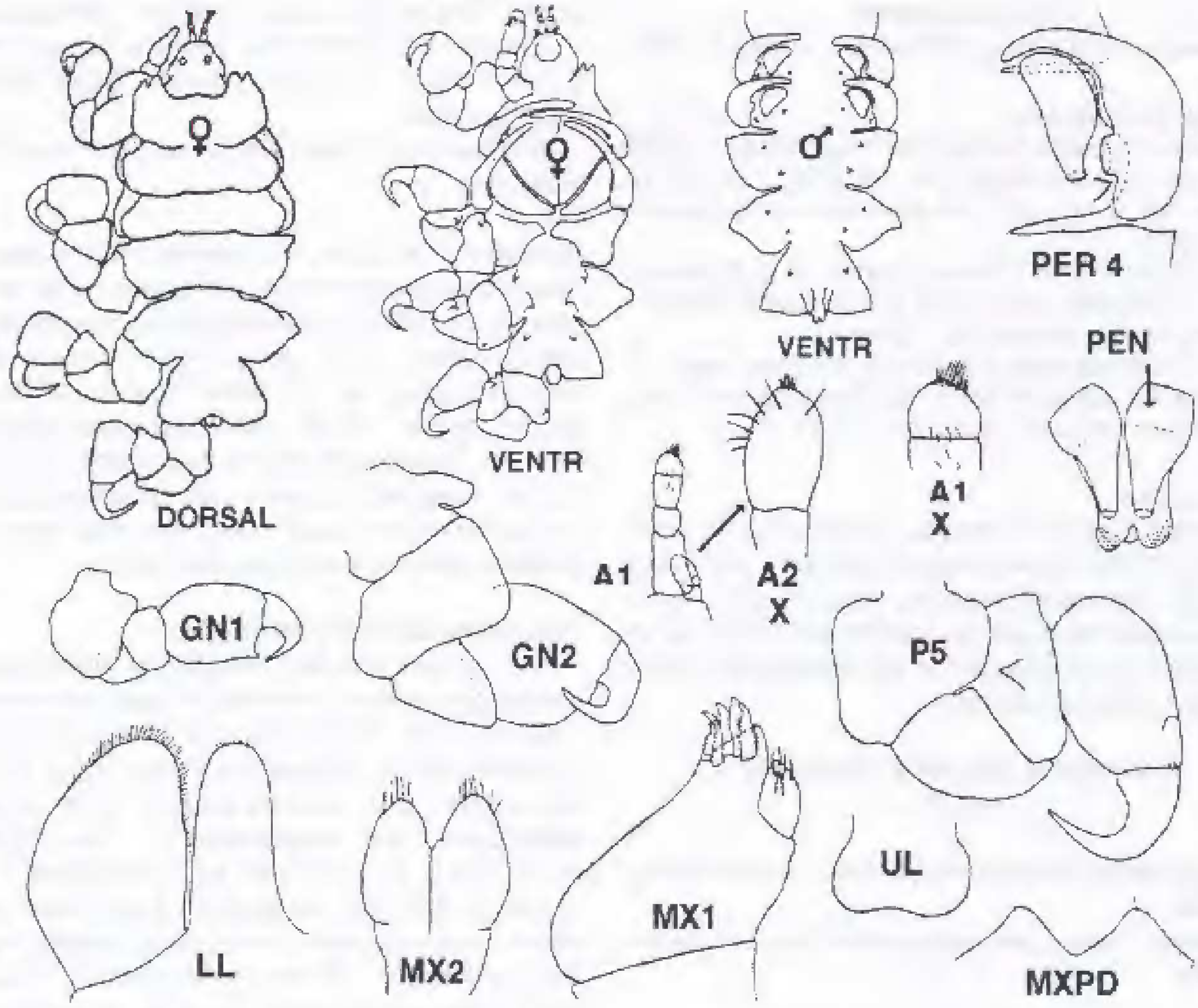

Fig. 27. ***Syncyamus pseudorcae*** **Bowman, 1955.** Male (4.0 mm); female (4.8 mm) ex *Pseudorca crassidens*, Gulf of Mexico (after Bowman 1955).

Antenna 1 very short, 4-segmented; antenna 2 minute, 2-segmented.

Mouthparts modified. Upper lip slightly incised apically. Lower lip, outer lobes approximating distally; inner lobes fused. Mandible, incisors multidentate, otherwise undescribed.. Maxilla 1, outer plate with 6 or 7 apical spine-teeth. Maxilla 2, inner plate fused totally within outer plate. Maxillipeds fused basally, each a low conical mound; segment 3 and palp lacking.

Gnathopod 2 medium large and stout, 5-segmented; propodal palm distinct, vertical; dactyl strongly curved, not pectinate, unguis not distinct. Gnathopod 2 stout, powerful, 4-segmented; propodal palm distinct, vertical.

Coxal gills single, short, thick, tapering, on peraeon segments 3 & 4; a single pair of accessory gills present in male.

Peraeopods 5-7 short, stout, powerful, appearing 5-segmented, segments 2 & 4 with antero-ventral adhesion spines.

Male penes stout, tapering distally diverging slightly. Pleopods shallowly, separated distally.

Remarks: The definition of this genus is problematical. Bowman's orginal figures of the type species *Syncyamus pseudorcae,* reproduced here (Fig. 27), indicate that gnathopod 1 is attached to fused peraeon segments 1 & 2 (demarcated by an antero-lateral marginal notch). Comparable figures for *S. aequus* (Lincoln and Hurley 1981; Mariniello et al. 1994) show the lateral marginal notch, but are otherwise ambiguous; in the ventral view of the male, the point of attachment is not shown; in the female, the point of attachment is indicated as the head proper, despite any suggestion of a posteriorly broadened head region. To clarify this problem, careful re-examination of type material is recommended.

Syncyamus species

Bowman, 1958; Leung, 1970a; Lincoln & Hurley 1981.

Material Examined:

Mediterranean Sea (locality indet.), ex *Delphinus delphis* - 3 specimens (identified by L. Margolis for Dr. Gallien, Dec. 1966 & Aug. 1971; specimens sent to Dr. Leung May 18, 1971).

Off Pacific coast of Mexico (locality indet.), ex *Tursiops* sp. - 2 specimens, identified for D. Rice, March, 1965. (See Leung 1967, p. 280 & 1970, p. 244.)

Guadalcanal (locality indet.), ex *Delphinus delphis* - 5 specimens (identified for Torben Wolff, February, 1964; specimens sent to Dr. Leung, May 18, 1971).

Remarks:

Material of *Syncyamus* sp., examined by Dr. Margolis in 1964, was no longer available for the current study. Species of *Syncyamus* occur mainly on warm-water dolphins (Table I, p. 110; Bowman 1958) and are unlikely to be collected in the northeastern Pacific region, north of California.

Scutocyamus Lincoln & Hurley, 1974

(Fig. 28)

Type species: *Scutocyamus parvus* Lincoln & Hurley, 1974.

Species: *Scutocyamus antipodensis* Lincoln & Hurley, 1980.

Diagnosis: Male (2.4 mm)

Body small, short, stout; widest at peraeon segments 5 & 6; peraeon segments 3 & 4 small, fused, narrowed in male; segments 6 & 7 fused dorsally. Peraeon segments 5-7 ventral adhesion spines.

Head very short. Antenna 1 very short, 3-segmented. Antenna 2 minute, 2-segmented.

Mouthparts: Upper lip slightly notched apically. Lower lip, outer lobes moderatey separated; inner lobes fused. Mandibular molar small, rounded, lacking proximal seta; incisor 5-cuspate; left lacinia 2-3 dentate, right lacinia bifid? 1-2 blades on each side. Maxilla 1, outer plate with 6 apical spine-teeth. Maxilla 2, inner plate fused within outer plate. Maxilliped, basal segments fused, lobe subacute, segment 3 and palp lacking.

Gnathopod 1 very small, 5-segmented; propodal palm lacking; dactyl irregularly pectinate distally, (combs of teeth), unguis not defined. Gnathopd 2 short, thick, powerful, appearing 3-segmented.

A single pair of coxal gills on each of peraeon segments 3 & 4, held crosswise; accessory gills lacking.

Peraeopods 5-7 short, stout, 5-segmented; segments 2-5 each with 1-2 ventral adhesion spines; dactyl strongly curved.

Female (ov.) (3.1 mm). Brood lamellae fringed with short setae.

Remarks: The genus *Scutocyamus* exhibits mainly apomorphic character states. Its members are ectoparasitic on small, fast-swimming Delphinoidea, especially dolphins of the genera *Lagenorhynchus* and *Cephalorhynchus* in the North Atlantic and North Pacific regions. In the short, squat powerful body form and fused peraeonal and limb segments *Scutocyamus* superfically resembles the apomorphic genus *Syncyamus* whose species occur on other types of Delphinoidea (see Table I and Discussion).

Discussion and Conclusions

The species of cyamid amphipods and their recorded cetacean hosts, treated in this study, are listed in Table I (p. 110). Some of these have been previously recorded from the northeastern Pacific region (*), or are expected to occur there because of the known distribution of host whale species (!). The latter includes *Orcinocyamus orcinus*, *Isocyamus kogiae*, *Syncyamus pseudorcae*, and possibly *Scutocyamus* spp. which are ectoparasitic on cold-water dolphins (e.g., *Lagenorhynchus*). However, two species, *Cyamus (Mesocyamus) mesorubraedon*, and *C. (Apocyamus) eschrichti*, proved new to science and two others, *Cyamus (Mesocyamus) orubraedon* and *Cyamus (Cyamus) monodontis* are apparently new to the region. Further new distributional records may be anticipated through close examination of little-studied host whales, including the common Orca, Dall's, and Harbour porpoises. However, new records from large, slow-moving, commercially valuable whale species (rorquals, right whales) are much less likely. Closer attention might be paid to ectoparasites of stranded ziphioid whales, and smaller whale species that are held captive in marine aquaria.

The evolutionary history of the cyamid amphipods is inextricably inter-related with that of the host Cetacea. Ancestral Cetacea almost certainly became aquatic prior to the evolution of the Cyamidae from an ancestral group within the Amphipoda Caprellidea. In attempting to reconstruct these events, we may first examine the possible ancestry and phylogeny of the Cyamidae within the Caprellidea, followed by a "best consensus" phyletic grouping of families within the

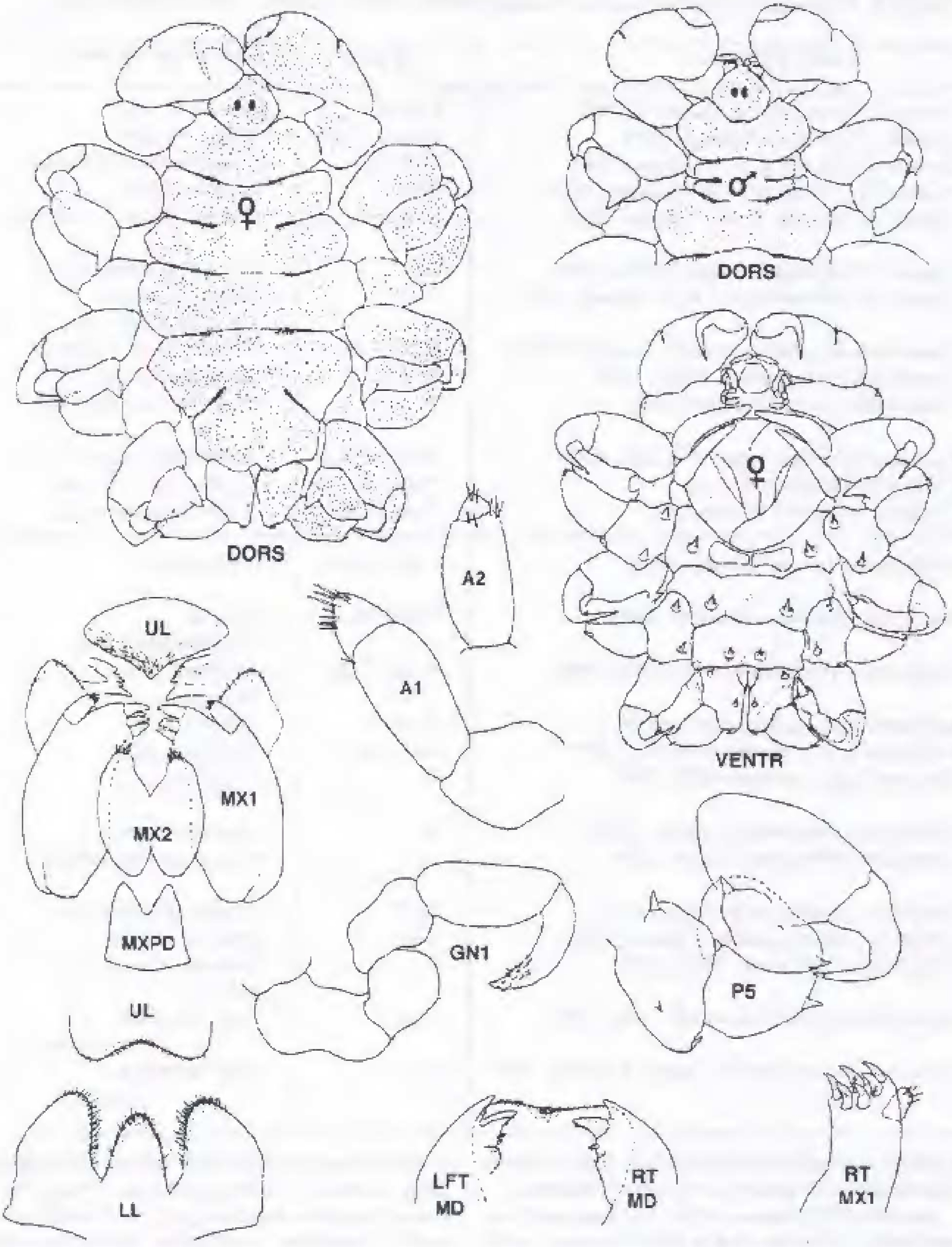

Fig. 28. ***Scutocyamus parvus*** **Lincoln & Hurley, 1974.** Male (2.4 mm); female (3.1 mm), ex *Lagenorhynchus albirostris*, North Sea. (after Lincoln & Hurley, 1974).

TABLE I. Whale lice (Cyamidae) and host Cetacea mainly of the northeastern Pacific marine region.

Family Cyamidae	**Region**	**Host Whale Species**
Cyamus (Cyamus) ceti (L.) Lamarck, 1801	P-A-At	Bowhead, Gray
Cyamus (C.) nodosus (Lütken, 1870)	P (Ber)-A -At	Beluga, narwhal
Cyamus (C.) ovalis R. de Vauzème, 1834*	P (SE AL)	N. Right whale (*B.glacialis*)
Cyamus (C.) erraticus R. de Vauzème, 1834*	P (BC)	*Balaena glacialis*
Cyamus (C.) gracilis R. de Vauzème, 1834*	P (SE AL)-At	N. Right whale *(B. glacialis)*
Cyamus (Paracyamus) boopis Lütken, 1870*	P-A	*Megaptera navaeangliae*
Cyamus (P.) balaenopterae K. H. Barnard, 1931*	P-At	*Balaenoptera* spp. (blue, fin, minke, etc.)
Cyamus(Mesocyamus) catodontis Margolis, 1954*	P (BC)-At	*Physeter macrocephalus*
Cyamus (M.) orubraedon Waller, 1989	P	*Berardius bairdii*
Cyamus ***(M.) mesorubraedon*** **n. sp.**	P	*Physeter macrocephalus*
Cyamus (Apocyamus) scammoni Dall, 1872*	P (AL-CAL)	*Eschrichtius robustus*
Cyamus ***(A.) eschrichtii*** **n. sp.**	P (Be - S. Cal)	*Eschrichtius robustus*
Cyamus (A.) kessleri Brandt, 1872*	P (AL-CAL)	*Eschrichtius robustus*
Orcinocyamus orcini (Leung, 1970)!	P (BC+?)-At	*Orcinus orca*
Neocyamus physeteris (Pouchet, 1888)*	P (SE AL-BC)	*Physeter* *Phocoenoides truei?*
Isocyamus delphini (Guérin-Méneville, 1836)	P (AL-CAL)	*Delphinus, Steno* *Globicephalus*
Isocyamus globicipitis (Lütken, 1873)	P-At	*Globicephalus*
Isocyamus kogiae Sedlak-Weinstein, 1992!	P (Austr)	*Kogia breviceps*
Isocyamus spp. (Bowman 1955, 1958)!	P	*Phoecenoides sp.*
Platycyamus flaviscutatus Waller, 1989*	P	*Berardius bairdii*
Platycyamus thompsoni (Gosse, 1855)	At	*Hyperoodon ampullatus*
Syncyamus pseudorcae Bowman, 1955!	At, P	*Pseudorca crassidens*
Syncyamus aequus Lincoln & Hurley, 1981	SAt	*Delphinus delphis*
Syncyamus sp. (Bowman 1955, 1958)*	P	*Tursiops, Grampus* *Stenella*
Scutocyamus parvus Lincoln & Hurley, 1974!	P-At	*Lagenorhynchus albirostris*
Scutocyamus antipodiensis Lincoln & Hurley, 1980	P-At	*Cephalorhynchus hectori*

Cetacea, and finally compare the two phyletic family classifications for possible correlative similarities.

Laubitz (1993) was one of few who attempted to relate family Cyamidae to other family groupings within the Caprellidea (Fig. 30). She viewed the Caprellidea as a polyphyletic group encompassing 8 distinct families. Four families were grouped within a "Paracercopidae" lineage, presumably derived from a leucothoid ancestral type. The other four families were grouped within a "Caprogammaridae" lineage that includes the widely dominant pan-boreal littoral marine family Caprellidae, presumably derived through a corophi-oidean ancestry. The first grouping is morphologically distinguished by a mandible with 6-toothed incisor, variable setal row, and lacks a molar; maxilla 1 has 6 spiniform apical "setae" (spine-teeth) and the

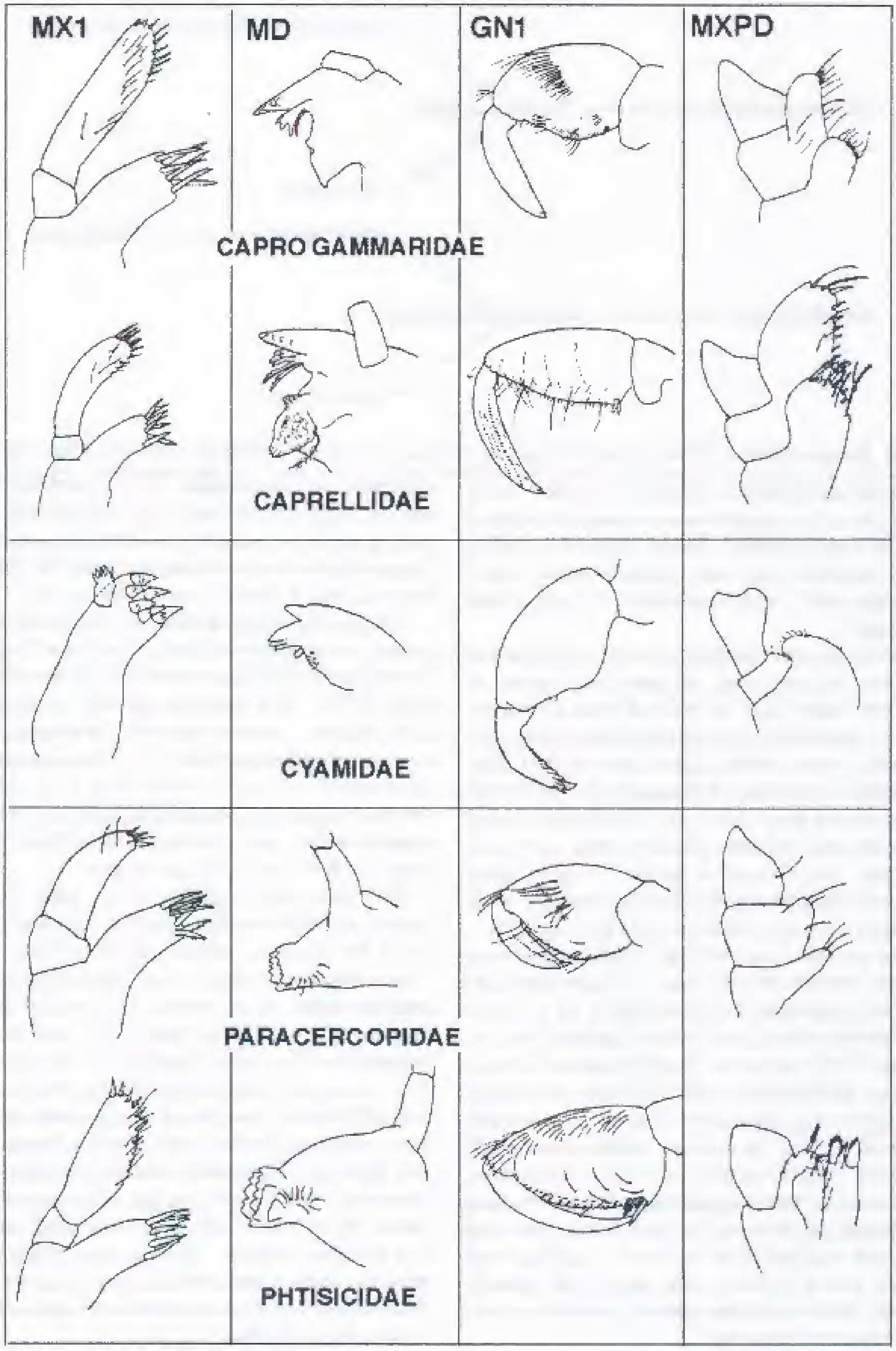

Fig. 29. Selected characters and character states of family Cyamidae in comparison with those of major family groupings withion Caprellida (after Laubitz, 1993).

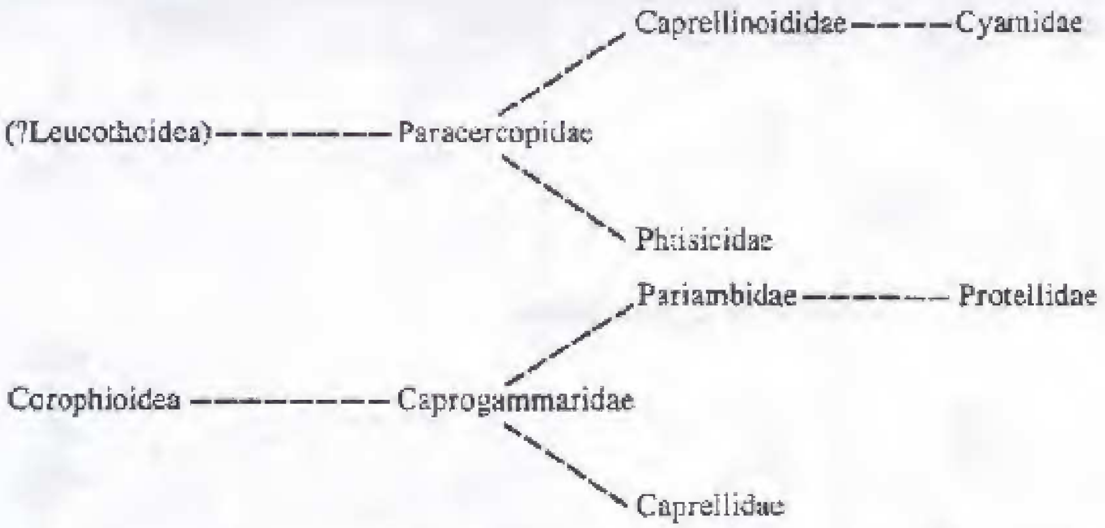

Fig. 30 Representation of hypothetical lines of evolution within Caprellidae (after Laubitz 1993).

maxilliped has a distinctive (larger) inner plate. In the second group, the mandible has a 5-cuspate incisor, a setal row of no more than 3 blades, and a strong molar process; moreover, the outer plate of maxilla 1 has 7 apical spine-teeth and the outer plate of the maxilliped is the larger.

However, in examing these characters and character states over a broad range of species and genera of Cyamidae studied here, these correlations are not immediately apparent and/or encounter many exceptions. In balance, more cyamids appear closer to the Caprogammarid line in having a 5-dentate incisor, few blades in the setal row, and a molar that is variously reduced but present, and plesiomorphically bears a proximal molar seta. As often as not, maxilla 1 bears 7 apical spine-teeth (plesiomorphic?), and the outer lobe of the maxilliped may occasionally exceed the inner lobe.

Other evidence suggests that cyamids were more probably derived directly from the caprogammarid line. Thus, gnathopod 1 of cyamids (Fig. 29, p. 111) is clearly hatchet-shaped and the dactyl straight; also, the abdomen is very similar to that of the genus *Caprella*. Moreover, the ancestral cyamid would almost certainly have occurred in the shallow littoral zone wherein chances of "fouling" an ancestral whale species would presumably have been relatively high. By contrast, members of the Paracercopidae line are more frequent in sublittoral depths where an air-breathing ancestral whale host was less likely to occur. Lacking fossil evidence, and/or rDNA genetic analogs, the question of cyamid derivation within suborder Caprellidea therefore remains problematical.

The ancestry of the Cetacea has been summarized neatly by Berta & Sumich (1999). Fossil physeteroids, ziphioids, and mysticetids occur somewhat further back in Tertiary times than do the delphinoids. Morphological, fossil, and rDNA evidence suggest that the Physeteroidea are more closely related to the primitive Mysticeti that to the advanced Delphinoidea.

The phenogram of character state similarities within genera and subgenera of family Cyamidae (Fig. 31) is derived by modified cluster analysis (see Bousfield and Shih 1994). This methodology may be considered semi-phyletic since the "states" of 24 selected characters are ordered phyletically, viz., plesiomorphic = 0, apomorphic = 2, and intermediate = 1. Selected characters encompass peraeon segments (3), head (3), mouthparts (9), gills (2), and gnathopods and peraeopods (7) (details available on request).

The "plesio-apomorphic" (P.-A.) index for each taxon is derived by totalling the ordered values for each of the 24 characters, with a maximum value of 48. Thus, subgenus *Cyamus* is here considered the most primitive taxon (P.-A. index = 11), and *Scutocyamus* the most advanced (P.-A. Index = 43), with other taxa intemediate. The separate treatment of the three "species" of *Isocyamus* appears justified by their character state differences; these are of a magnitude similar to those separating the subgenera of genus *Cyamus*. The new genus *Orcinocyamus* is nearly as distinct from the *Isocyamus* complex as is the genus *Neocyamus*. The genera *Platycyamus* and *Syncyamus* seem naturally (but distantly) related. *Scutocyamus* would appear relatively closely similar to *Syncyamus*, but the homoplasious nature of these similarities is suggested by the dotted connecting line.

The phyletic "trees" of both cyamids and whales (Figs. 31, 32) may now be compared. In general the

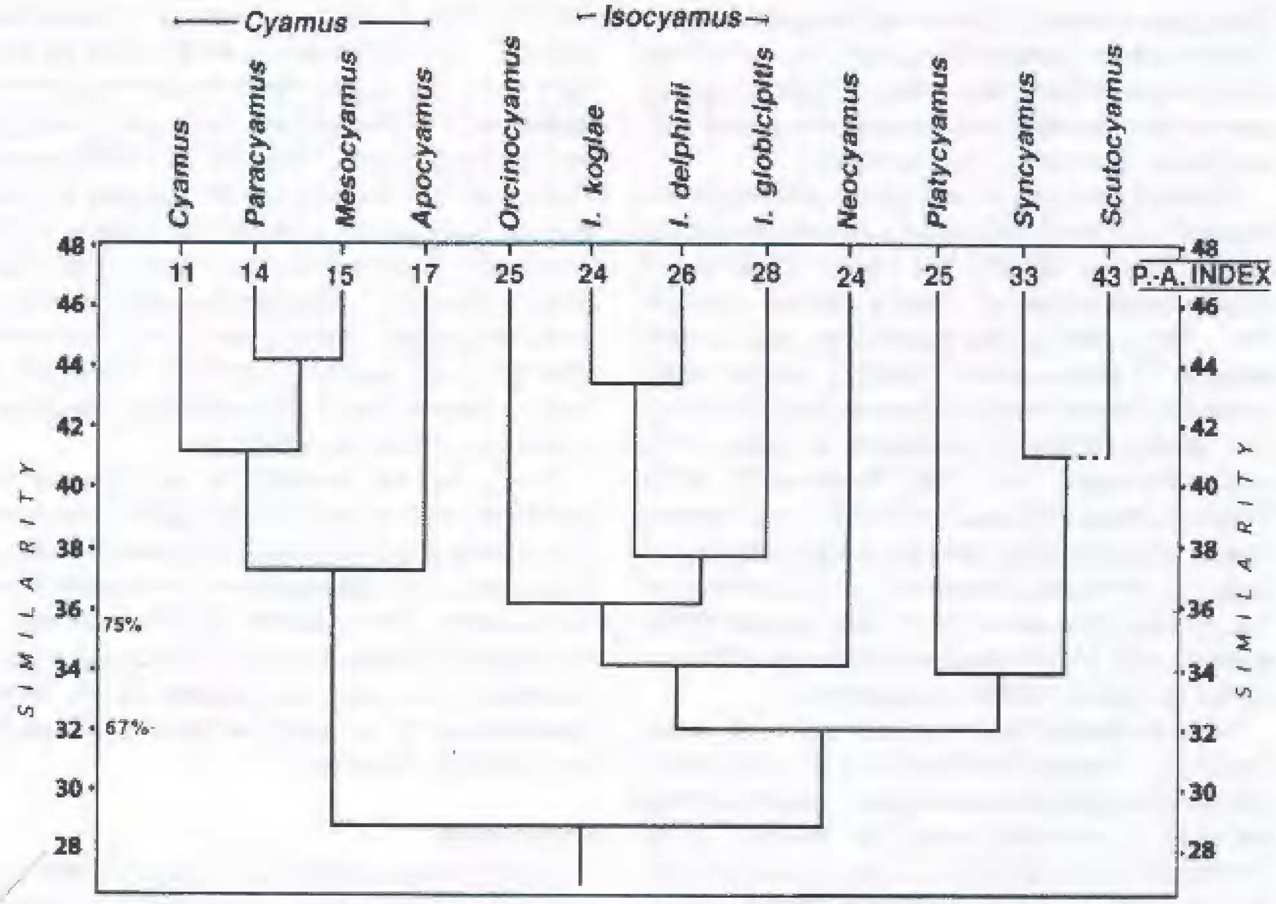

Fig. 31. Phenogram of hypothetical relationships between genera and subgenera of Cyamidae.

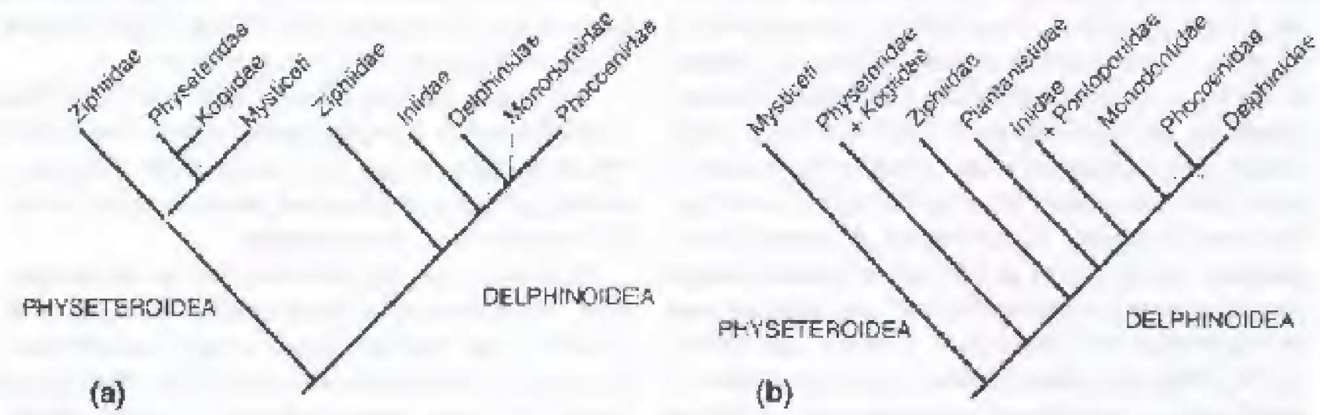

Fig. 32. Hypothetical relationships of extant mysicetid-odontocetid whales based on (a) cyto chrome b sequence data; (b) morphological data (after Berta & Sumich 1999).

correlation is reasonably good. Thus, species of the primitive genus *Cyamus* (and subgenera) occur mainly on the primitive Mysticeti, some on the primitive Odontoceti (Ziphiidae, Physeteridae,and Monodontidae), but none on the advanced Delphinoidea. On the other hand, the advanced ectoparasitic genera (*Isocyamus, Orcinocyamus, Scutocyamus* and *Syncyamus*) occur only on the Odontoceti and not on the primitive Mysticeti.

Further analysis of the relationships between supergroups and families within the Cetacea (Fig. 32) provides a basis for comparison with the phyletic classification of cyamid ectoparasites. Berta and Sumich (1999) indicate that the Physeteridae and Ziphiidae, having modified double blowholes, are more closely related to the Mysteceti, having double blowholes (primitive condition), than to the Delphinoidea, having single dorsal blowholes (advanced condition).

The former are host to species of the primitive genus *Cyamus* and the intermediate genera *Neocyamus* and *Platycyamus* whereas the advanced Delphinoidea are host to the more advanced ectoparasitic genera *Orcinocyamus*, *Isocyamus*, and *Syncyamus*.

Although discovery of new species of cyamids continues slowly, partly because of a current moratorium on the whaling industry, the known occurrence of cyamid ectoparasites on Cetacea remains relatively low. Thus, although the mammalian order Cetacea contains 76 extant species (Berta & Sumich 1999), cyamid ectoparasites have been recorded from only 34 host species (Leung 1967; Lincoln & Hurley 1981; Sedlak-Weinstein 1991, 1992; Wardle et al. 2000). This constitutes only about 40% of the total cetacean fauna . Not surprisingly, the known frequency is much higher in the more commercially valuable Mysticeti [i.e., from all but one of the 11 host species (90%)] whereas only 23/65 species of Odontoceti (32%) are known to harbour cyamid ectoparasites.

Some reasons for these low frequency levels may be historical. First and foremost is the low commercial value of the smaller cetacean species, so that most were not taken or examined during the "hey-day" of the commercial whaling industry. Many odontocete species, especially among the 19 species of beaked whales, are very rarely stranded or taken in oceanic long-lines, and are fast-moving and difficult to capture, even for use in marine aquaria. Thus, material of cyamids from common fast-swimming coastal whales of British Columbia, e.g., the closely related Dall's and Harbour porpoises, and the long-lived Orca (see Hoyt 1990; Spalding 1999) have been unavailable to the authors to date. Concerning known host species within the Mysticeti, the frequency of occurrence of cyamid ectoparasites may be as low as 4% (as recorded on flensed rorqual species at whaling stations) and therefore may be overlooked by collectors. Lincoln and Hurley (1974, 1980) opined that because some species of ectoparasites (e.g., *Scutocyamus parvus*) are very small and occur only around genital organs and blow holes, they are likely to be overlooked by all but the most careful collectors. About ten species of whales (within Platanistidae, Pontoporiidae, Iniidae, and Lipotidae) are restricted mainly to fresh waters of India, Brazil, and China, presumably posing intolerable physiological limitations to ectoparasitism by cyamids of strictly marine ancestry.

As noted above, some species of whales (e.g., *Megaptera*) apparently carry only one species, whereas others (e.g., *Eschrichtius*, *Balaena mysticetus*, *Physeter*) transport at least three species of cyamid ectoparasites. Collection data in the literature are sparse and inexact, but suggest that ectoparasite species may "partition" available surfaces and largely avoid interspecific competition. Thus, Waller (1989) notes that *Platycyamus flaviscutatis* occurs generally but singly over the body surface of *Berardius*, whereas *Cyamus orubraedon* is clustered around the tip of the xiphiid whale's lower jaw. Regrettably, notes of this type concerning cyamid material taken from *Eschrichtius*, *Physeter*, and *Eubalaena glacialis*, whales that are know to carry at least three ectoparasite species, were seldom provided by the collectors.

Finally, the uneven quality of taxonomy of some species of cyamids, some of which have been recorded from widely disparate groups of odontocete hosts, indicates that closer examination of ectoparasitic material is needed. For the present, however, we may conclude that knowledge of cyamid-cetacean speciation is insufficient for close interpretation of the phyletic classification of one group in terms of the phyletic classification of the other.

Conclusions

Some 24 species of cyamid amphipods were treated systematically of which two were new to science, and 6 others were new to the northeastern Pacific region. Two new subgenera were erected within genus *Cyamus* to encompass the diversity revealed by detailed examination of characters and character states.

The origin of family Cyamidae with the Caprellidea is problematical. Morphological evidence provided by character states across the present wide spectrum of cyamid genera and species of the study does not support current views on the subject.

In general, the phyletic classification of the Cyamidae corresponds reasonably closely with that of the Cetacea. An ordered character-state (semi-phyletic) phenogram of cyamid relationships (Fig. 31) suggests that phyletic relationships of cyamid genera and species corresponds to those of the host whale taxa (cf. Fig. 32). Thus, members of the most primitive genus, *Cyamus* (and subgenera) occur mainly on the most primitive groups of whales (Mysticeti) and none on the most advanced group of Odontoceti (Delphinoidea). Conversely, advanced genera of cyamids are found only on the advanced Odontoceti.

The cyamid fauna of the world is yet insufficiently studied to facilitate critical use of the group as a potential guide to the origin and evolution of the Cetacea.

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Table II. Abbreviations for Figures:

A1	-	**antenna 1**
A2	-	**antenna 2**
ABD	-	**abdomen**
ACC	-	**accessory**
ADHES	-	**adhesion**
BR PL	-	**brood plates**
COX	-	**coxal**
DORS	-	**dorsal**
GEN	-	**genital**
GN1	-	**gnathopod 1**
GN2	-	**gnathopod 2**
HD	-	**head**
JUV	-	**juvenile**
LAT	-	**lateral**
LFT	-	**left**
LL	-	**lower lip (labium)**
MD	-	**mandible**
MX1	-	**maxilla 1**
MX2	-	**maxilla 2**
MXPD	-	**maxilliped**
P5-7	-	**peraeopods 5, 6, 7**
PEN	-	**penis**
PER	-	**peraeon segment**
PLP	-	**palp**
PLPD	-	**pleopod**
RT	-	**right**
SP	-	**spine**
UL	-	**upper lip (labrum)**
X	-	**magnified**

DALL'S PORPOISE
Phocoenoides dalli